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Proceedings of the Sixth Southern Conference on Forest Tree Improvement

SCHOOL OF FORESTRY
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Gainesville

PROCEEDINGS OF THE
SIXTH SOUTHERN CONFERENCE ON
FOREST TREE IMPROVEMENT

School of Forestry
University of Florida
Gainesville, Florida

June 7 - 8, 1961

THE SIXTH SOUTHERN CONFERENCE ON FOREST TREE IMPROVEMENT

The Sixth Conference, sponsored by the Committee on Southern Forest Tree Improvement, was held June 7 - 8, 1961, on the campus of the University of Florida, Gainesville. The theme of the conference was "Ten Years of Progress".

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Philip A. Briegleb, Southern Forest Experiment Station

This is the twenty-first technical paper released under the sponsorship of the Committee on Southern Forest Tree Improvement.

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A Decade of Progress in Tree Improvement

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Tree improvement research has been a part of the scene in American forestry for over half a century. Only in the last decade, however, has major attention been directed to it. A careful examination of the historical record probably would reveal a number of factors that contributed to the awakened interest. Two, I think, are significant. First is the influence of a number of prominent foresters who attended the Third World Forestry Congress in Helsinki, Finland, in 1949. These men, among whom can be named Dr. I. T. Haig and J. Herbert Stone, had the background to understand the significance of the advances in tree improvement that were being made in Northern European countries. Their recognition of this significance permeated their associates. I recall that the Appalachian Section of the Society of American Foresters devoted its annual meeting in January, 1950, to tree improvement at the suggestion of Dr. Haig, who helped set up the program. The second factor was an exchange of correspondence, beginning in the fall of 1949, between the Forestry Relations Division of the Tennessee Valley Authority and the Southern Forest Experiment Station on the possibility of a regional seed source research program. As an outgrowth of this correspondence the two regional forest experiment stations and the regional office organized the First Southern Conference on Forest Tree Improvement, held in Atlanta on January 9 and 10, 1951.

Somewhat unexpectedly, about 80 people attended the conference. As a result of the deliberations, Dr. Haig and C. A. Connaughton were instructed to appoint a standing committee to coordinate forest tree improvement research and to prepare information on the subject. A twelve-member committee was appointed to include representation from research and regional federal forestry activities, state forestry agencies, the Tennessee Valley Authority, schools and industry.

At its first meeting this group assumed the name Committee on Southern Forest Tree Improvement. Early in its existence it adopted a four-point program of purposes and objectives:

1. To advise and assist those interested in the improvement of southern forest trees in arranging and conducting research and development programs.

2. To provide a clearing house for information on forest tree improvement.

3. To provide for or assist in coordination in the conduct of a South-wide program of tree improvement research and development.

4. To foster and encourage the advancement of knowledge of southern tree genetics.

In this Sixth Conference on Southern Forest Tree Improvement, advances in the tree improvement knowledge and practice will be presented. I shall summarize developments of the past ten years and point out the possible function of the Committee on Southern Forest Tree Improvement in these advances. Many people in public agencies and private industry have provided me with information. I am particularly indebted to Philip Wakeley and Dr. Keith Dorman for their accounts of happenings prior to 1951 and of the work of the Southern and Southeastern Forest Experiment Stations.

Early Studies

Wakeley points out that forest genetics work began in this country with studies of racial variation as related to geographic seed source. Tests were started with ponderosa pine in northern Idaho and in Colorado in 1916. Seed collection began in 1912 for an extensive study of Douglas-fir. Wakeley's 4-source loblolly study was established at Bogulusa, Louisiana, in 1925. Ernest Schreiner and others started an extensive poplar hybridization program in Maine in 1924. And in 1925, James G. Eddy started the Eddy Tree Breeding Station, now known throughout the world as the Institute of Forest Genetics, at Placesville, California.

The South

With this very brief resume, let us direct our attention to the South where extensive beginnings in tree improvement research had been made prior to 1951. Almost exclusively the activity was limited to the Southern and Southeastern Forest Experiment Stations and to T.V.A.

I have cited Wakeley's early study. He also did some crossing of pine species. The early work at the Lake City Research Center was done at a time when that center was still a part of the Southern Station. Most notable was the selection of high gum yielding slash and longleaf pine started in 1941 by Mitchell, Dorman and Schopmeyer. Rooted cuttings of nine high gum yielding clones and six average yielders were produced. By controlled and wind pollination of 12 high yielding and average trees a progeny plantation of 629 trees was established. From this study have come a number of important publications on forest tree improvement.

At the Southeastern Station, the Appalachian Station at that time, a large study with open pollinated loblolly pine was started in 1934 by A. L. McKinney and L.E. Chaiken. From the seed of each of 105 mother trees, 100 plantable seedlings were obtained and planted in four replications with 25 trees per plot. Early results of this study gave strong indications of rather wide inherent variation in loblolly pine. Flooding of the plantation by the Santee-Cooper power project terminated the study.

Leon Minckler established a pitch pine x loblolly pine hybrid plantation on the Lee Experimental Forest in Virginia in 1945. Also in that year he put in a racial variation study of loblolly pine from four geographic sources and shortleaf pine from five sources.

Under Dorman's supervision a cooperative program was started with the Ida Cason Callaway Foundation at Hamilton, Georgia, in 1949.

As a result of selection among wilt-resistant strains of mimosa in North Carolina, George Hepting and Richard Toole had 28 resistant clones by 1948. Several of these were given to the nursery trade and have carried forward the immunity to wilt. Hepting, Bratislav Zak, and others, in 1950 began making selections in shortlead pine for resistance to littleleaf disease.

The Tennessee Valley Authority started tree improvement studies in 1933 with the establishment of an experimental tree crop nursery at Norris Dam. Until 1949, the research was devoted mostly to selection and testing of improved nut trees and other crop trees suitable for planting on open land. Some limited attention was given to hardwood species suitable for timber production. Since 1944, collections have been made of trees with unusual and attractivily figured wood, including yellow poplar, red maple, walnut, hybrid poplar, and birch. In 1950, studies on pine tree improvement were started in which vegetative propagation and seed source tests were stressed. Attention has also been given to blight resistant chestnut of which seven selections have been propagated.

Developments Since 1951

T.V.A.

By 1960, T.V.A.'s selection and testing of crop trees had resulted in the planting of 140 black walnut, 184 chinese chestnut, 115 filbert and 31 pecan plantations on the lands of about 325 co-operators. Superior tree selections were started in 1957 with loblolly, shortleaf and Virginia pine. Other activities in the current program include seed source tests and studies on vegetative propagation.

Southern Station

Those of you who are intimate with developments in tree improvement know that both of the regional experiment stations have given tree improvement major attention since 1951. Wakeley's contribution to the Southwide Seed Source Study, started in the name of the Committee on Southern Forest Tree Improvement in 1951, has been outstanding. At the Crossett Research Center of the Southern Station the Crossett Company began financing a full-time researcher in tree improvement in 1952, carrying this support to the present. Changing the Gulf Coast Research Center at Gulfport into the Southern Institute of Forest Genetics, in 1954, firmly established the position of the Southern Station in this area of research. At the institute, with supplementary work at Crossett, Arkansas, Alexandria, Louisiana, and with Hodges Land and Timber Co., Inc., at Many, Louisiana, research is being carried on in southern pine hybridization; racial variation in southern pines; fundamental studies in forest genetics, including physiological investigations; and the inheritance of resistance to fusiform rust. Some beginnings have been made in hardwood genetics at Stoneville, Mississippi.

Southeastern Station

The Southeastern Station at the Lake City Research Center has continued the development of strains of superior gum yielding longleaf and slash pine. Tree selection techniques, vegetative propagation, and insect relationships, are a part of the program. At the Callaway Foundation, studies on selection techniques and inheritance have been continued. In cooperation with the Georgia Forestry Commission and Georgia Forest Research Council, seed orchard establishment has received major attention at Macon, Georgia. In addition to these continuing programs, a longleaf pine study was started in South Carolina in 1955; a yellow poplar study in North Carolina in 1954, also a hemlock study in 1957 and a white pine study in 1959. A slash pine study was started in Florida in 1954 and a loblolly study in Florida and Georgia in 1956.

In addition to the pitch pine x loblolly pine plantation mentioned earlier for the Lee Forest, the Southeastern Station has shortleaf x loblolly pine hybrids plus back crosses planted at the Hitchiti Experimental Forest and other hybrids at the Callaway Foundation.

The Southern Region, Region 8, of the U. S. Forest Service is planning for 650 acres of seed orchards by about 1963. Some 3000 acres of seed production areas will be used to supply seed until the seed orchards provide the necessary supplies.

Industry

A large part of the applied effort in forest tree improvement is carried on by the pulp and paper industry, usually in cooperation with a research center at a university or with one of the regional experiment stations. Several companies, however, do have independent programs in addition to participation in cooperative programs.

Credit for some of the very earliest work must go to the Westvaco Research Center of the West Virginia Pulp and Paper Co. Here L. T. Easley, P. T. Lannon, and others, were making seed collections from selected trees as early as 1950 and at about that time began the establishment of a series of seed production areas in outstanding stands of loblolly pine.

The Buckeye Cellulose Corporation under the direction of Donald Stevenson has been doing tree improvement work as part of a broader research program since 1954. Current studies are concerned with chemical and physical characteristics of slash pine wood, racial variation in slash pine, and growth chamber evaluation of open-polinated plus tree slash pine progeny.

At the Southlands Experimental Forest, the International Paper Company has made tree improvement a part of the research program. Projects are concerned with heritability in pines, seed orchard pruning, seed orchard irrigation, species variation, and the introduction of exotics.

Other companies that have given considerable attention to tree improvement are Union Bag-Camp Paper Corp., Gaylor Division of Crown-Zellerbach, and the Crossett Company. A number of others are doing very fine work within the limits of the resources that they can devote to this activity.

Industries are giving financial support to tree improvement research as well as providing land and assigning personnel toward broadening the effectiveness of research agencies. The program of the Texas Forest Service is receiving support from nine companies. The School of Forestry at North Carolina State College is being assisted by 13 companies. Nine companies are cooperating in the program of the University of Florida.

The industries in the cooperative program of N. C. State College and the University of Florida are basically concerned with the establishment of seed orchards. This has led to the selection of well over a thousand mother trees. The principal species have been slash and loblolly pine; however, selections of shortleaf, pond and Virginia pines have also been made. Several companies are making plans for programs with longleaf and sand pine, and possibly also hardwoods. At present between 1,300 and 1,400 acres of seed orchard are in place in individual orchards comprising from 15 to over 50 clones. Current projections provide for well over 2000 acres of orchard. A number of companies are limiting their projections until part of the task of progeny testing has been accomplished and until research more clearly defines procedures and possibilities in tree improvement.

State Agencies

Except for the Texas Forest Service, state agencies in the South do not carry out research; hence, tree improvement activity is restricted to seed orchard and seed production area establishment. Texas did initiate tree improvement research in 1951, as part of a broader research program. As pointed out in the Eighth Progress Report for the program, the original objectives remain basically unchanged and are (1) to develop strains of pine capable of yielding increased volumes of straighter, higher quality timber than is now being grown, (2) to develop a drought resistant strain of loblolly pine to expand the pine region and for use on adverse sites, and (3) to develop pine strains with naturally high or low wood density.

Seven states have some seed orchard acerage. Georgia started in 1954 and plans for 450 acres. Florida, beginning in 1959, now has 46 acres and expects to have about a 1000. Alabama has plans for 10 acres. Kentucky has two acres and expects to put in 10 in cooperation with T.V.A. Louisiana has projected 60 acres over the next three years. Texas has 20 acres with plans for 90 -- mostly loblolly and slash pine. Virginia expects to expand the present loblolly acreage of 30 to about 65 and the nine acres of shortleaf to 20. Thought has been given to a white pine orchard. Several states have seed production areas.

Schools

Among the schools and state agricultural experiment stations Florida led off in 1952 with the appointment of Dr. Tom O. Perry. The program was expanded in a major fashion in 1954 with the organization of a cooperative industry supported program pointed primarily toward tree selection and seed orchard establishment. Inheritance of individual characters, racial variation and techniques of vegetative propagation were other areas of study. At present, various aspects of seed orchard management, heritability studies, and plot size studies for progeny tests are receiving major emphasis.

North Carolina State College launched an industry supported program in 1956. This has been promoted vigorously and effectively. At first, emphasis was on aspects of seed orchard establishment and heritability of wood characteristics, particularily specific gravity. The program has become quite diverse and now includes studies on heritability in loblolly pine; physiological studies on growth, photosynthetic efficiency, and respiration; characteristics of trachieds; seed orchard studies; hybridization; and including a number of studies on variation and heritability with hardwoods, particularily yellow poplar and sweet gum. These studies in an extensive graduate teaching program are a real factor in extending the breadth of the research.

The University of Georgia initiated her program in 1954. It now includes work on heritability of southern pines, vegetative propagation, graft survival, and factors significant in the selection of breeding stock. Plans for more extensive physiological studies are being made.

Auburn University has given some attention to tree improvement since 1953, beginning with geographic seed source studies. Increasing emphasis is being given to physiological studies on characteristics of seedlings of selected pines.

Louisiana Polytechnic Institute, Mississippi State University, Louisiana State University and the University of Arkansas have limited studies emphasizing geographic variation.

The University of Tennessee started a program in 1959 that now includes studies on variation and heritability of yellow poplar and breeding studies with yellow poplar, chestnut, and a number of other hardwoods.

In 1953 the University of Florida, with the help of the Texas Forest Service and the Southern Station, held a short course on tree improvement. Succeeding courses were held at Lufkin, Texas; Florida; Athens, Ga.; and Raleigh, N. C. These courses provided basic training for a large number of the foresters now envolved in one fashion or another in southern forest tree improvement.

Professional Manpower in Tree Improvement

Among the state agencies, Georgia has four foresters devoting most of their time to seed orchard and tree improvement work. Alabama has two part-time; Florida one full-time. Louisiana has one man who spends much of his time in the work. Virginia has two men full-time. Texas, more concerned with research, has a geneticist with the Ph. D., a second man with an M. S. and has plans for the employment of a physiologist.

Within industry some 10 or 12 men appear to be devoting full time to tree improvement. However, many foresters possibly 40 to 60, or more, have some direct responsibility in tree improvement other than that of administration or general supervision. In many companies the identification of outstanding trees that might possibly serve as superior mother trees is a permanent assignment of all foresters who work in company forests.

The Southern Forest Experiment Station at the Southern Institute has six people assigned full time to tree improvement. Wakeley devotes some time to this work. There is one man at Crossett as previously pointed out, two part-time at Stoneville, Mississippi, and one part-time at Alexandria. To sum up, there are 13 researchers of whom 6 are full-time and at least two others better than half-time.

Four men devote full time to tree improvement for the Southeastern Station - two at Lake City and two at Macon. In addition, tree improvement is carried on part-time by one man at Cordele, Georgia; two at Charleston, S. C.; one at Franklin, Virginia; two at Charlottesville, Virginia; one at Asheville, North Carolina; two at Athens, Georgia; and one at Lake City.

T.V.A. has one full-time worker in tree improvement.

Among the schools, Florida has three full-time staff members on tree improvement research. North Carolina State has four. Georgia has two and two others part-time. Auburn has the equivalent of about three full-time. Tennessee has one full-time and two part-time. Louisiana Polytechnique Institute, Louisiana State University, and Arkansas, have one or more staff members who are doing some work in tree improvement.

In the aggregate this becomes at least 48 full-time workers in some phase of tree improvement research or development and development.

Summary of Activity

The basic effort thus far has been in the development of seed orchards and in related supplementary research. Species variation, heritability, breeding, and hybridization are all receiving attention. A most encouraging aspect of the developing research program is the increasing emphasis that is being given to the fundamental physiology-biochemistry of tree growth, including aspects particularly pertinent to forest tree genetics, by the Southern and Southeastern Forest Experiment Stations, N. C. State College, Auburn University and Georgia.

The Committee on Southern Forest Tree Improvement has expanded its membership from the original 12 to 18, and has been active in the assignments to which it set itself. At two-year intervals it has sponsored a southwide conference. It has brought out 20 publications and reports, including the proceedings of the previous conferences, through the facilities of the employing organization of various members. A committee newsletter, scheduled for semiannual publication, has appeared annually with 450 copies for a mailing list of about 250. At the request of the Southern Forest Experiment Station, the Committee became advisory to the Southern Institute of Forest Genetics in 1955 and holds meetings at the Institute on an irregular schedule.

The effective influence of the southern committee has resulted in the organization of tree improvement committees in the Northeast, the Lake States, and the West.

In this decade of development, the influence of the Committee has been felt in the adaptation of practices, in the initiation of research, in the creation of a public consciousness of the importance of tree improvement, and in the acceptance of tree improvement as a part of industrial forest management. In the Committee's short lifespan, we have seen the genetical improvement of forest trees advance from a scientific oddity to an honored position in forestry research and practice.

We now have ten years of developmental experience. We are beginning to form the reservoir of knowledge on the fundamentals of tree growth on which we must draw to further our research. The potential for progress is the challenge that lies ahead in forest tree improvement. Our attainments will depend on the financing and intellectual inspiration that we can bring to focus on the problem.

RESULTS OF THE SOUTHWIDE PINE SEED SOURCE STUDY
THROUGH 1960 - 61

Philip C. Wakeley[1]

Southern Forest Experiment Station

Forest Service, U. S. Department of Agriculture

The Southwide Pine Seed Source Study was launched by the Committee on Southern Forest Tree Improvement in 1951 to delimit practicable seed-collecting zones for longleaf (Pinus palustris, Mill.), slash (P. elliottii elliottii, Engelm.), loblolly (P. taeda, L.), and shortleaf (P. echinata Mill.) pines. It was established and is being maintained entirely by the generous and painstaking cooperation of numerous Federal, State, educational, and industrial agencies. It includes seed from and plantations in 16 States, from Pennsylvania and New Jersey south to Florida and west to Missouri, Oklahoma, and Texas.

Nine plantations of slash pine and 19 apiece of longleaf, loblolly, and shortleaf were established in 1952-53 and 1953-54 with stock from 1951 and 1952 seed. Each seed source in the study was represented in either 1 or 2 plantations close to that source. For slash pine, 3 supplementary plantations were established outside the species' range.

Rainfall was deficient in most of the southern pine region during both 1953 and 1954, and some of the plantations suffered severely from drought. Losses were greatest in longleaf and shortleaf. Fresh collections of seed of these 2 species were accordingly made in 1955, duplicating as nearly as possible the 1951 and 1952 collections, and 29 new longleaf plantations and 33 new shortleaf plantations were established in 1956 - 57 and 1957 - 58. Some of these new plantations replace earlier ones that failed; the rest constitute immensely informative replications, in time and place, of the earlier ones that survive.

Of the total of 128 plantations established in the study, 108 have survived well enough to justify reexamination on schedule[2].

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[1] Chairman, Subcommittee on Geographic Source of Seed, Committee on Southern Forest Tree Improvement.

[2] A tabular summary of plantations, by species, dates of establishment, and suitability for continued remeasurement, appears on page 6 of the Proceedings of the Fifth Southern Conference on Forest Tree Improvement. See also the explanatory note in the second full paragraph on page 7 of those Proceedings.

Before results can be presented, one special feature of the plantations must be mentioned. This is that, except with slash pine, the geographic seed-sources represented in each year's planting of each species are grouped in 2 or 3 series.

Each series consists of from 6 to 9 sources representing either 2 north-and-south transects of the species' range or 1 east-and-west transect. Each such series has at least 1 seed source in common with each other series of the same species planted in the same year. These sources-in-common serve to link the various series together.

The series were instituted mainly to conserve seed supplies and to relieve cooperating planters of the burden of planting unduly large acreages. They were designed to test definite hypotheses concerning the origin and distribution of racial variation -- the north-and-south transects, for example, to test the hypothesis that racial variation is associated mainly with differences in temperature. As things have worked out, the series constitute an unexpectedly powerful analytical tool as well.

The immediately pertinent data on the 108 successful plantations consist -- in addition to voluminous establishment records and special notes -- of either 3 or 4 observations apiece of some 136,000 measurement trees, or upwards of 500,000 observations in all.

When the preliminary report on 5-year results was presented at the Fifth Southern Conference (Wakeley 1959), fewer than 5 percent of these data had been analyzed. Now routine analysis is 92 percent complete. Since the Fifth Conference, analyses of variance have been made of 397 out of 432 available reexaminations of survival and height--mostly by IBM-704, but in a few instances by hand. Thirty-five analyses remaining to be made by hand involve either missing-plot technique for which a suitable IBM program is lacking, or complications arising from replacements of dead trees.

This report presents the 5-year results of the original plantings and the 3-year results of the supplementary plantings from 1955 seed. Information at later ages is not yet available, as the next regular periodic reexamination is not due in any of the plantations until 1961-62.

Caution Necessary in Drawing Conclusions

Five years' growth in plantations is not enough to justify final conclusions regarding the suitability or unsuitability of seed from various sources for use in specific localities.

Weidman (1939), in his article on evidences of racial influence in ponderosa pine, offers a classic example of the pitfalls involved in too early evaluation of seed-source plantations. He describes a study of 19 geographic sources of ponderosa pine seed, planted on the Kaniksu National Forest, in northern Idaho. At 10 years--twice the age of the oldest trees in the present report--the stock of Coconino origin excelled all but 1 of the other stocks in height, and equalled that one. The square outlined in the lower left-hand corner of figure 1 shows the course of growth of the Coconino and 3 of the other stocks over the first 10 years. The easy assumption at this stage would have been that the Coconino source was best adapted to the site.

Figure 1.-- Height growth of geographic sources of ponderosa pine planted on Kaniksu National Forest (after Weidman, 1939).

By the end of the twentieth year, however, the height of the Coconino stock, as shown in the main part of figure 1, had dropped below the heights of the 3 stocks that the Coconino had equalled or excelled at 10 years. It had dropped below 9 of the other 15 stocks in the study, as well. Obviously, a favorable rating of the Coconino stock, based on the first 10 years' growth, would have been premature.

There is no evidence whatever that some of the southern pine sources that top the lists in the analyses presented here today may not, by the next reexamination, fall behind like Weidman's Coconino stock.

Occurrence of Significant Variation in Southern Pines at 5 and 3 Years

Nevertheless, certain significant differences in survival and height that have already developed in the Southwide Study cannot be disregarded. Moreover, there are indications of a consistent pattern among successive plantings of the same species, and among different species.

The least evidence of this pattern is afforded by the slash pine plantations. Survival varies significantly (5-percent level) with seed source in 71 percent of the plantations; very

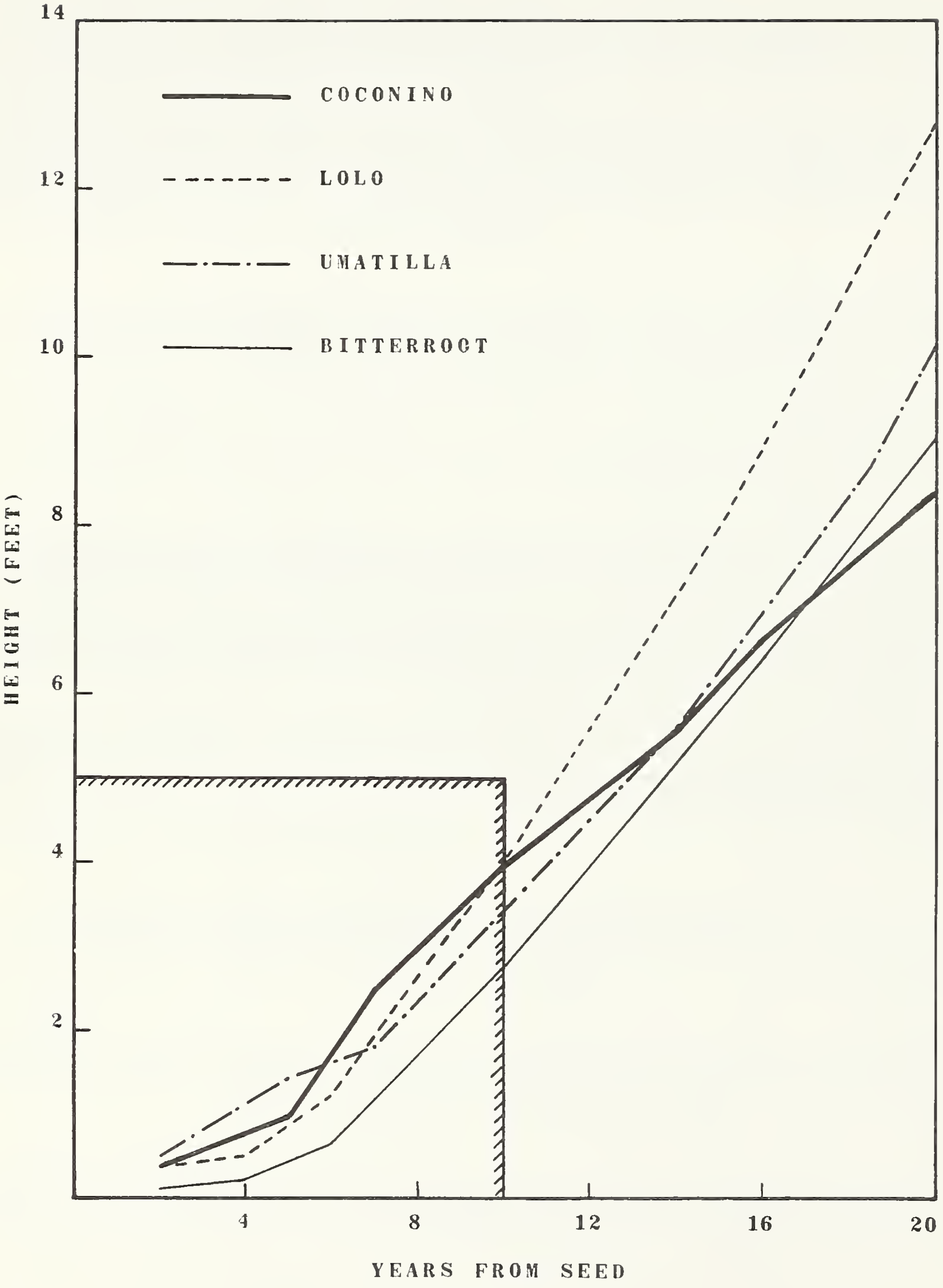

Figure 1.--Height growth of geographic sources of ponderosa pine planted on Kaniksu National Forest (after Weidman, 1939).

significantly (1-percent level) in 57 percent. The corresponding percentages for significant variation in height are 14 and 29. As a group, though, both the slash seed sources and the slash plantations are the least satisfactory in the entire study. Even more important, all but 1 or possibly 2 of the significant differences are attributable to a single seed source, from the lower part of the Florida peninsula. Apparently the pollen parents of some of the seedlings representing this source were South Florida slash pines (P. elliottii densa Little and Dorman), and poor survival and growth of the resulting inter-varietal hybrids may have accentuated the differences between the southern Florida and the other slash pine stocks.

If the atypical stock from this southern Florida source is discounted, the slash pine included in the study has exhibited less racial variation during the first 5 years, in either survival or height, than any of the other 3 species.

Many of the longleaf plantations exhibit significant or highly significant variation from source to source, in survival, height, or both, but the variations must be interpreted cautiously.

Of the 19 longleaf plantations established in 1952-53 and 1953-54, only 9 have been successful enough to justify reexamination as scheduled; and in some of these the survival pattern was seriously modified by the unavoidable use of stock of some sources from one nursery and of other sources from another. In other words, physiological quality of stock, attributable to nursery soil or nursery treatment, may have outweighed geographic source of seed in its effect on survival; in a few plantations there is clear evidence that this is true. The 5-year heights may also have been modified by nursery sources of the stock; and in the plantations characterized by slower average growth, average heights have excessive experimental errors because of individual-tree variations in the onset of height growth.

More of the longleaf plantations established in 1956-57 were successful, and in the great majority of them all the stocks in 1 plantation are from 1 nursery. The 3-year heights of these plantations--the latest heights available--have, however, even larger experimental errors than the 5-year heights of the older plantations, because of the characteristically irregular onset of height growth of longleaf pine.

Figure 2A shows the extent of significant variation in survival and height of the earlier

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Figure 2.-- Extent of significant variation in survival and height of longleaf pine. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

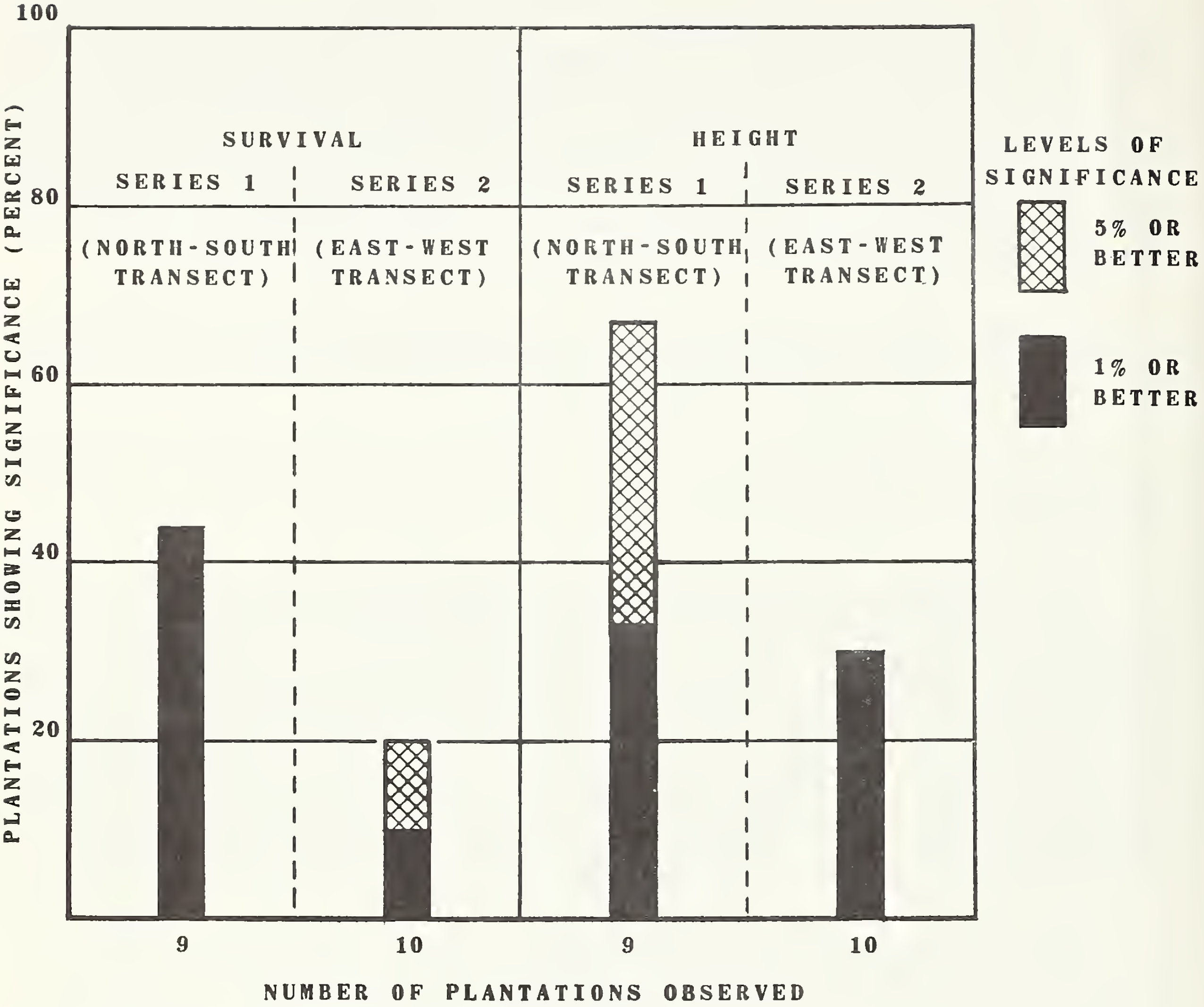


Figure 3.--Extent of significant variation in survival and height of loblolly pine at 5 years.

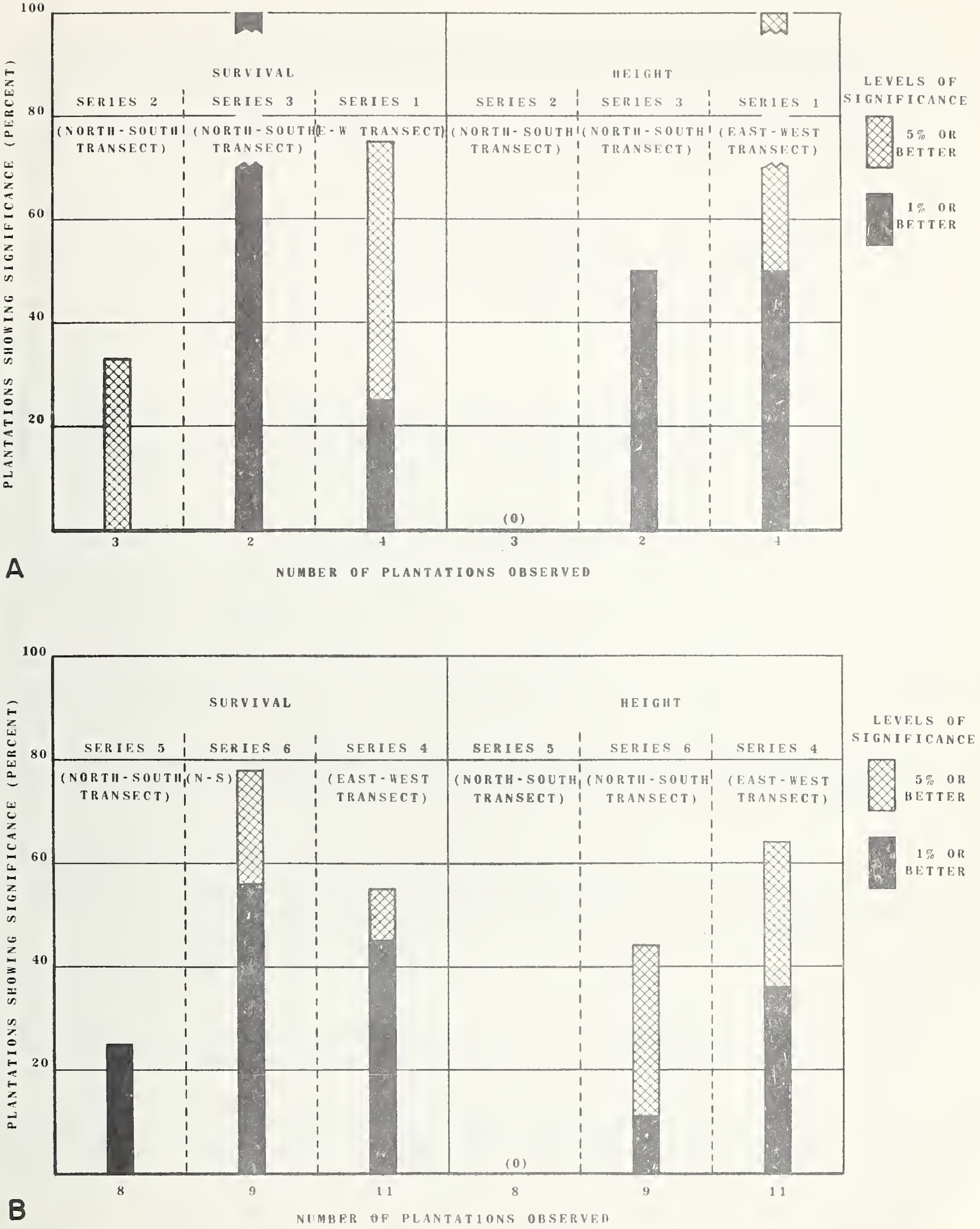


Figure 2.--Extent of significant variation in survival and height of longleaf pine. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

longleaf plantations. Much significant variation occurs in the series representing sources along an east-west transect of the species range, but part of it is definitely attributable to nursery influence. Relatively little significant variation--none in height--occurs in connection with one of the north-south transects, but much highly significant variation occurs in the other.

Figure 2B, based on many more later longleaf plantations, essentially confirms the pattern indicated in the earlier plantings. The 3 transects duplicate almost exactly those shown in figure 2 A. As in figure 2 A, sources representing the east-west transect vary greatly in survival and in height. Those representing one north-south transect vary greatly; those representing the other do not.

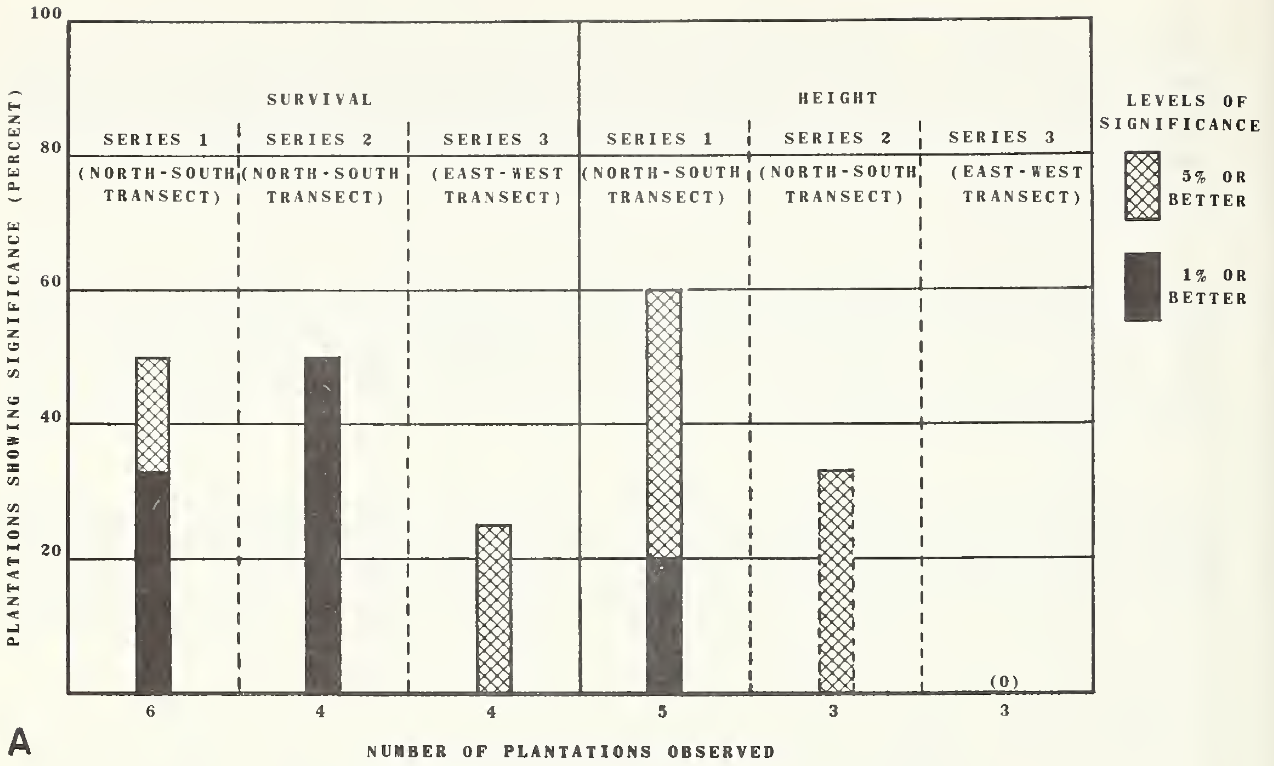
In loblolly pine, the pattern is simpler. Loblolly Series 1 consists of sources representing north-south transects of the species range; Series 2, of sources representing a roughly east-west transect, along the isotherm of 62°-63° F. mean annual temperature. As figure 3 shows, significant variation in both survival and height is much more common among sources ranging from north to south than among those ranging from east to west.

Figure 3.-- Extent of significant variation in survival and height of loblolly pine at 5 years.

Figure 4 A shows the same pattern in shortleaf pine at 5 years as in loblolly at 5 years. Significant variation in both survival and height is consistently more frequent among the plantations containing sources along the north-south transects than among the plantations containing sources along the east-west transect.

Figure 4.-- Extent of significant variation in survival and height of shortleaf pine. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

Figure 4 B shows the occurrence of significant variation at 3 years in the 3 shortleaf series planted in 1956-57. Series by series, the sources duplicate in part the sources in



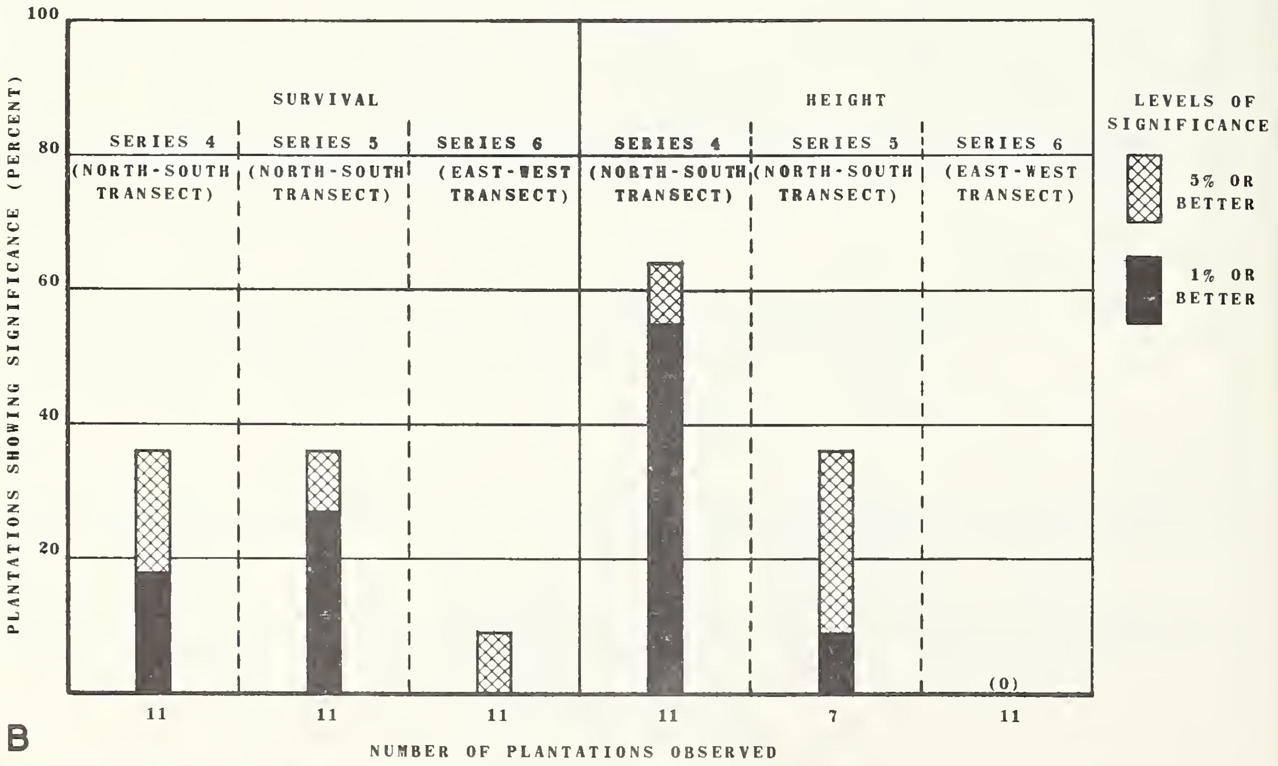


Figure 4.--Extent of significant variation in survival and height of shortleaf pine. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

the earlier plantations, but, because of fluctuations in seed supply, a few of the original sources had to be replaced by new ones. Despite these substitutions, the pattern of variation is essentially the same as that shown in figure 4 A: frequent significant variation, in both survival and height, among sources ranging from north to south, and little or none among sources ranging from east to west.

The foregoing results suggest that, when local seed is unavailable, it may be better to get seed from sources east or west of the planting locality than from sources farther north or south. The 5-year-old loblolly plantations and the 5 and 3-year-old shortleaf plantations indicate that both survival and height of stocks from farther north or south are more likely to differ significantly from those of local stocks than are the survivals and heights of stocks originating farther east or west. The longleaf plantations confirm the suggestion only in part, as east-west variation is greater and north-south variation is less than in loblolly and shortleaf, but, as has been pointed out, the results with longleaf merit less weight, for several reasons. The results with slash pine lend little weight to the suggestion, but do not conflict with it in any way.

A special note about loblolly pine is in order. Although survival and height vary less significantly among sources ranging from east to west than among those ranging from north to south, susceptibility to fusiform rust varies more from east to west, especially in the central and southern parts of the species' range (Henry 1959). Stock from eastern sources is more susceptible than that from western sources. With loblolly pine, therefore, substitutes for local seed probably should be obtained from west of the planting locality, rather than north, south, or east. This will be discussed in more detail later.

Local versus Other Individual Sources

Discussion so far has been in terms of the "series" described in connection with the longleaf, loblolly, and shortleaf components of the Southwide Study, and of the generally more frequent occurrence of significant variations in the series representing north-south transects of the species' ranges.

As each series representing an east-west transect of a species' range in linked to 1 or 2 north-south series by 1 or more common seed-sources, stocks from the seed-sources used as links have been planted more or less widely throughout the species' ranges. Their survivals and heights throughout the species' ranges can therefore be compared with those of stocks from sources local to the various plantations. In the paragraphs that follow, comparisons are made in terms of the frequency with which survivals or heights excel over-all averages of individual plantations, or are best in individual plantations. Frequencies are expressed as percentages of all plantations in which the specified stocks have been observed.

It may be stated at the outset that stock from local seed, especially of longleaf, has by no means always proved best at the end of 3 to 5 years. It has not always been above average for the individual plantation. In a number of plantations the local stock has survived or grown less well than any other. In evaluating these facts, it must be remembered that: (1) Many of the differences between local and other stocks fall far below the 5-percent level of significance, especially in the series representing east-west transects; and (2) with longleaf, some of the differences in survival are directly attributable to nursery rather than to genetic influences, and many of the differences in height are associated with excessively high mean squares for error. With these 2 reservations in mind, some of the differences between local and selected individual sources merit discussion.

Figure 5 A compares the performance of local longleaf stocks, at 5 years, with those of individual stocks representing (within a narrow range of latitudes) longitudes of 80°, 83°, 88°, and 93° W

Figure 5.-- Comparison of survival and height of local longleaf stocks with those of widely planted stocks representing individual sources. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

Local stocks had average or better survival in a far smaller percentage of plantations than did the stocks from longitudes 88° and 93° W.

In height, local stocks made a somewhat better showing but were still surpassed by the stocks from longitudes 83° and 88° W. In fact, in plantations well distributed over the longleaf pine range, stock from longitude 88° W. excelled local stocks in both survival and height.

The most striking thing about Figure 5 A, however, is that the 83° west longitude stock had lower than average survival wherever planted, but made average or better growth in a higher percentage of plantations than did local stock. By contrast, the 93° west longitude stock had above-average survival wherever planted, but above-average growth in a smaller percentage of plantations than local stock.

Figure 5 B makes similar comparisons for the 1956-57 longleaf plantations at 3 years. The 4 individual stocks compared with local stocks are essentially the same as in figure 5 A.

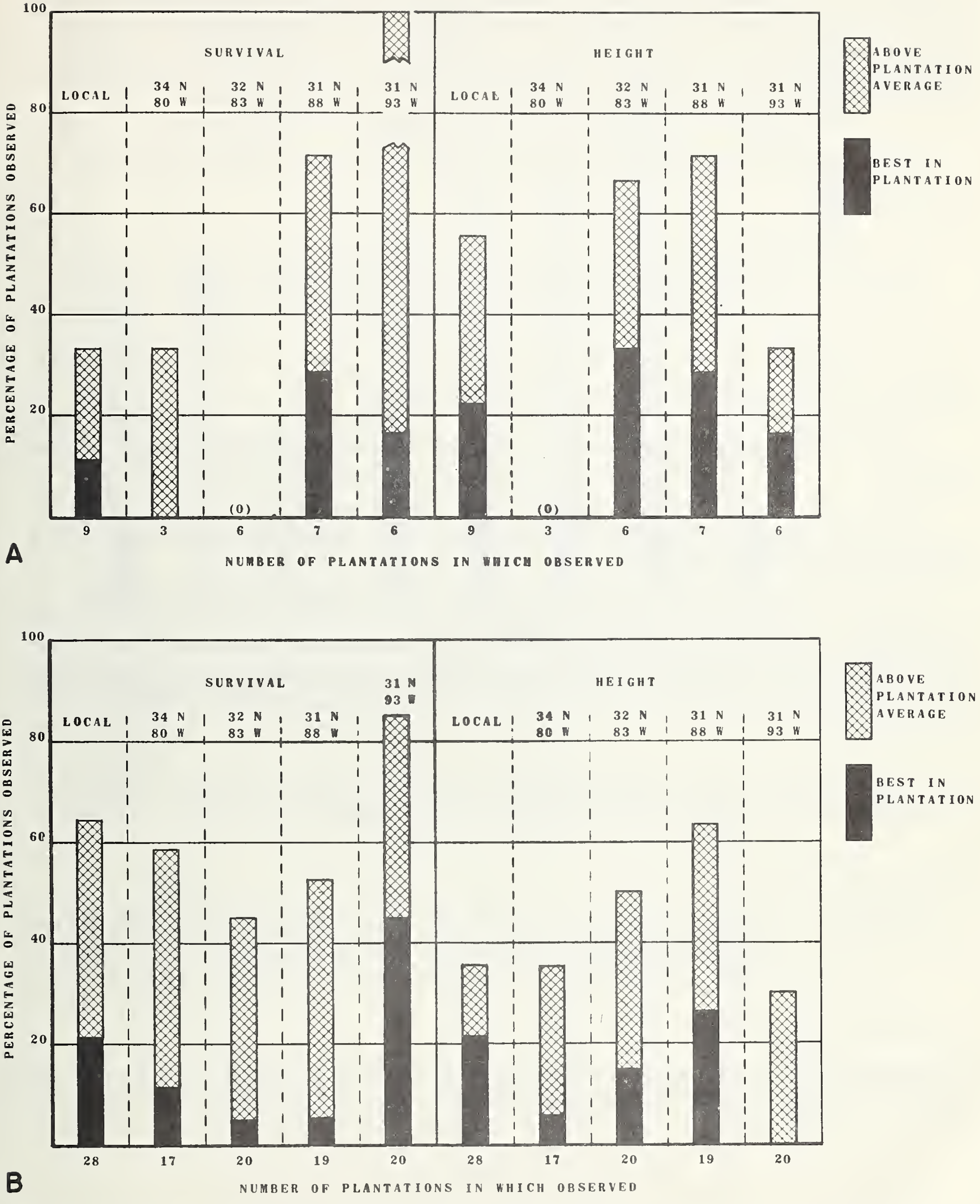


Figure 5.--Comparison of survival and height of local longleaf stocks with those of widely planted stocks representing individual sources. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

Contrasts are less extreme, as might be expected from the history of establishment and the age of the trees. Local stocks show up more favorably in survival and less favorably in height than in figure 5 A. Again, however, the stock from longitude 83° W. has fallen behind the local in survival but has excelled it in growth, and the stock from longitude 93° W. has excelled the local in survival but fallen below it in growth.

Figure 6 compares local loblolly stocks at 5 years with 3 other stocks representing longitudes of 77°, 91°, and 93° W., at various latitudes.

Figure 6.-- Comparison of survival and height of local loblolly stocks, at 5 years, with those of widely planted stocks representing individual sources.

On the whole, local loblolly stocks performed considerably better than local longleaf stocks.

One individual loblolly stock, from longitude 77° W., equalled or excelled the local stocks in both survival and height.

Again, individual stocks excelled local stocks in one characteristic and fell behind them in the other. The stock from longitude 91° W. survived less well than the local but made better height growth. The 93° west longitude stock survived far better than the local but made average or better height growth in a far smaller percentage of all plantations in which observed.

In shortleaf at 5 years, local stocks make the best showing yet observed (figure 7 A). Even here, however, the growth of 1 individual stock, from longitude 85° W., although not equalling that of local stocks, was relatively better than its survival, and the survival of another, from longitude 92° W., although inferior to that of local stocks, was relatively better

Figure 7.-- Comparison of survival and height of local shortleaf stocks with those of widely planted stocks representing individual sources. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

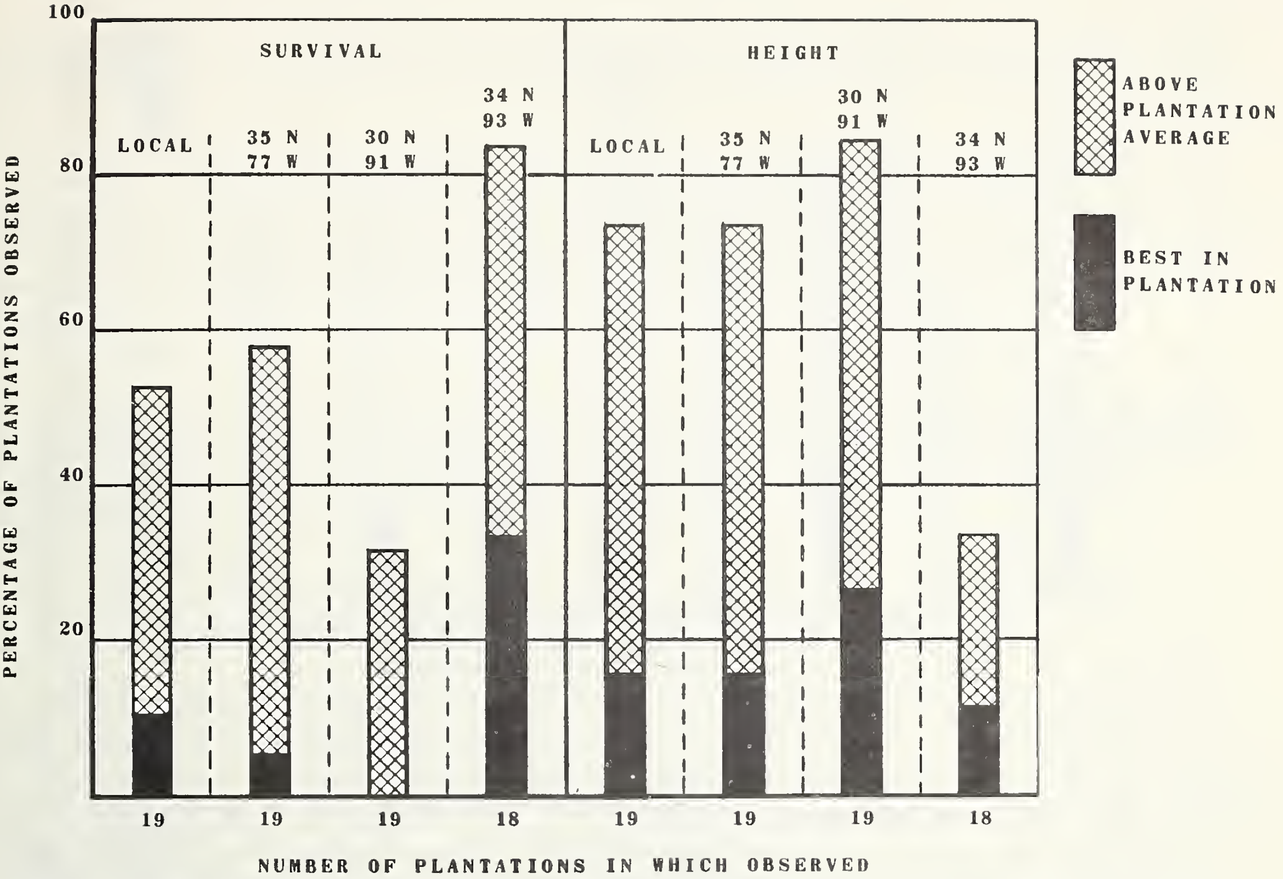


Figure 6.--Comparison of survival and height of local loblolly stocks, at 5 years, with those of widely planted stocks representing individual sources.

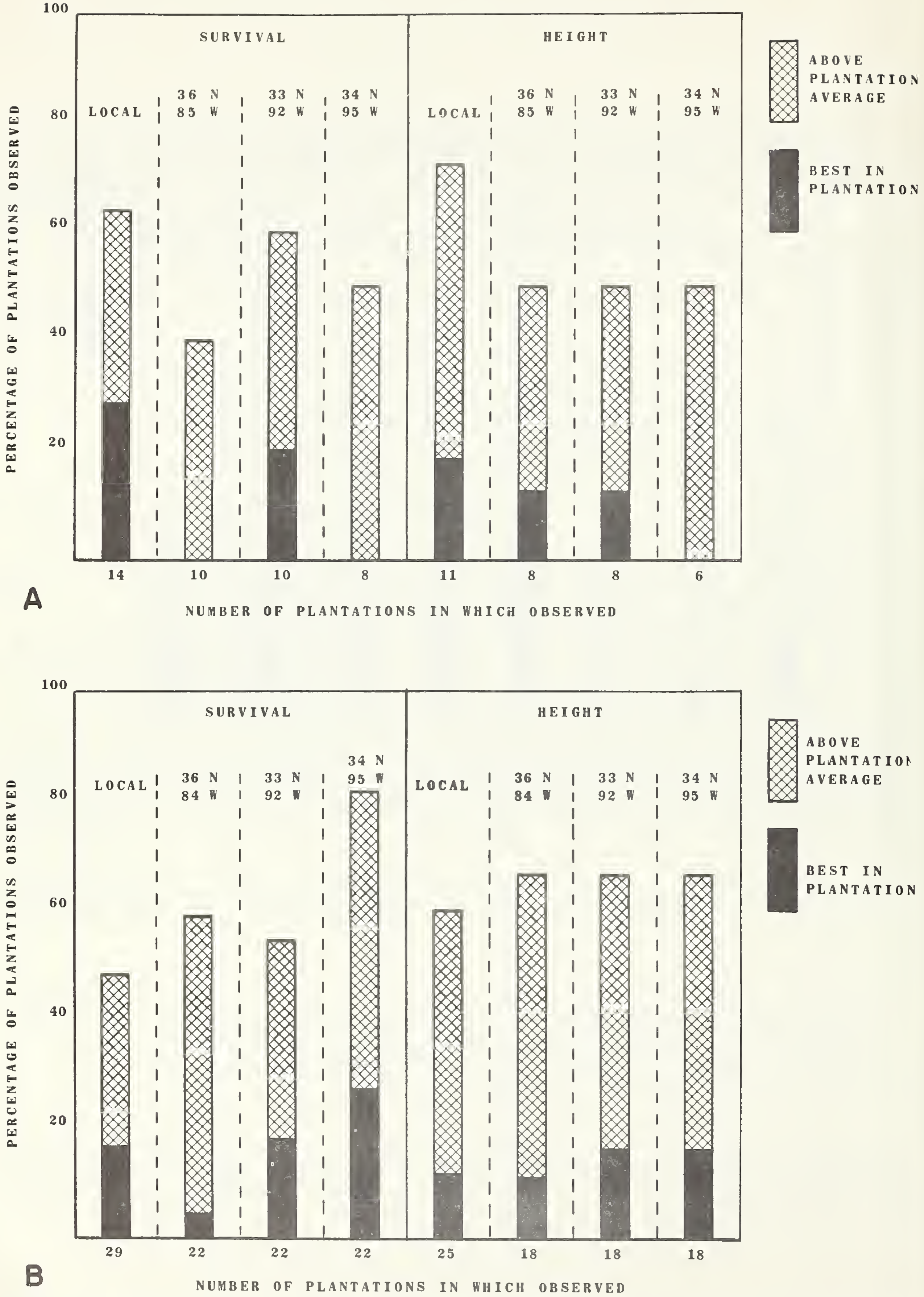


Figure 7.--Comparison of survival and height of local shortleaf stocks with those of widely planted stocks representing individual sources. A, in 1952-53 and 1953-54 plantations at 5 years; B, in 1956-57 plantations at 3 years.

than its growth. For some unknown reason the stock representing the most westerly source, longitude 95° W., did not survive outstandingly well in the original shortleaf plantations.

In the 1956-57 shortleaf plantations, at 3 years, the stock from longitude 95° W., survived outstandingly well (figure 7 B), being above average in a far larger percentage of plantations than local stocks, but its growth was only slightly better than that of local stocks, and was less good than its survival. Local stocks make a relatively poor showing in figure 7 B, perhaps because the trees were too young to show the adaptability of the local stocks in figure 7 A.

In figures 5 through 7 as a group, most of the individual stocks showing better survival but poorer growth than local stocks are from seed sources in the western part of the species ranges. Most of those showing better growth but poorer survival are from southern or eastern sources.

More Detailed Evaluations of Individual-Source Relationships

The comparisons in figures 5 through 7 are in very general terms. They include non-significant as well as significant variations in survival and height. The plantations observed are not uniformly distributed over the species' ranges; a majority of them are in the lower latitudes. Lastly, more by accident of seed supply than anything else, most of the individual stocks with which local stocks are compared represent east-west transects of the species' ranges. This preponderance of east-west comparisons minimizes attention to variation in a north-and-south direction, which figures 2 through 4, and especially 3 and 4, show to be more frequently significant. Adequate evaluation of the more important north-and-south variation requires a different form of analysis.

Figure 8 shows the mean 5-year heights of loblolly pine of 8 sources, in 2 plantations, plotted over latitudes of source.

Figure 8.-- Mean heights of loblolly stocks at 5 years, over latitudes of seed sources, in northern and southern plantations.

In the Pearl River County, Mississippi, plantation, at latitude 30° 44' N., there is a negative regression of 5-year height over latitude of seed source. The slope falls somewhat

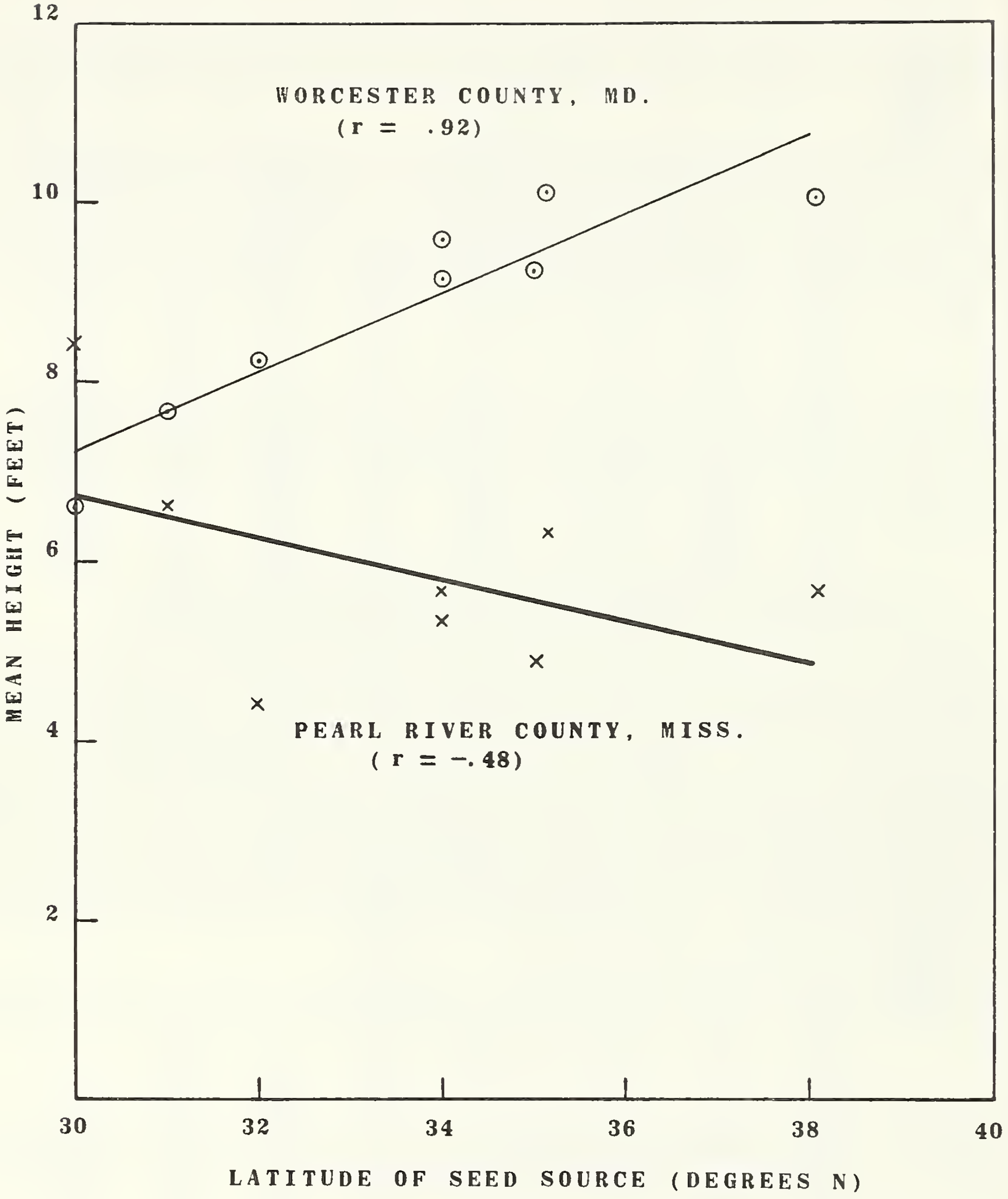


Figure 8.--Mean heights of loblolly stocks at 5 years, over latitudes of seed sources, in northern and southern plantations.

short of significance at the 5-percent level. The coefficient of correlation is -.48.

The same stocks in the plantation in Worcester County, Maryland, at latitude 36° 35' N., show a strong positive regression of 5-year heights over latitude of source. The degree of slope is highly significant, and the coefficient of correlation is +.92.

The striking thing about figure 8 is the reversal of the slope of the curve when stocks representing a north-south transect of the species' range are planted near opposite ends of the transect.

The 1952-53 and 1953-54 shortleaf plantations do not afford quite so good an example of this reversal of slopes, because all the northern-most plantations failed. Nevertheless, figure 9 suggests the same trend. Seven stocks planted in St. Helena Parish, Louisiana, at latitude 30° 58' N., show a highly significant negative regression of 5-year heights over latitude of seed source; the coefficient of correlation is -.97. The same stocks planted in Morgan County, Tennessee, at the intermediate latitude of 36° 00' N. (and an elevation of 1,280 feet) show a non-significant positive regression of 5-year height over latitude of source, with a coefficient of correlation of only +.34.

Figure 9.-- Mean heights of shortleaf stocks at 5 years, over latitudes of seed sources, in plantations at southern and intermediate latitudes.

Figure 10 shows the same relationship as figures 8 and 9, in terms of 3-year heights of younger shortleaf plantations.

Figure 10.-- Mean heights of shortleaf stocks at 3 years, over latitudes of seed sources, in plantations at northern, southern, and intermediate latitudes.

In figure 10, 7 stocks planted in Washington Parish, Louisiana, at latitude 30° 42' 30" N., show a highly significant negative regression of 3-year height over latitude of seed

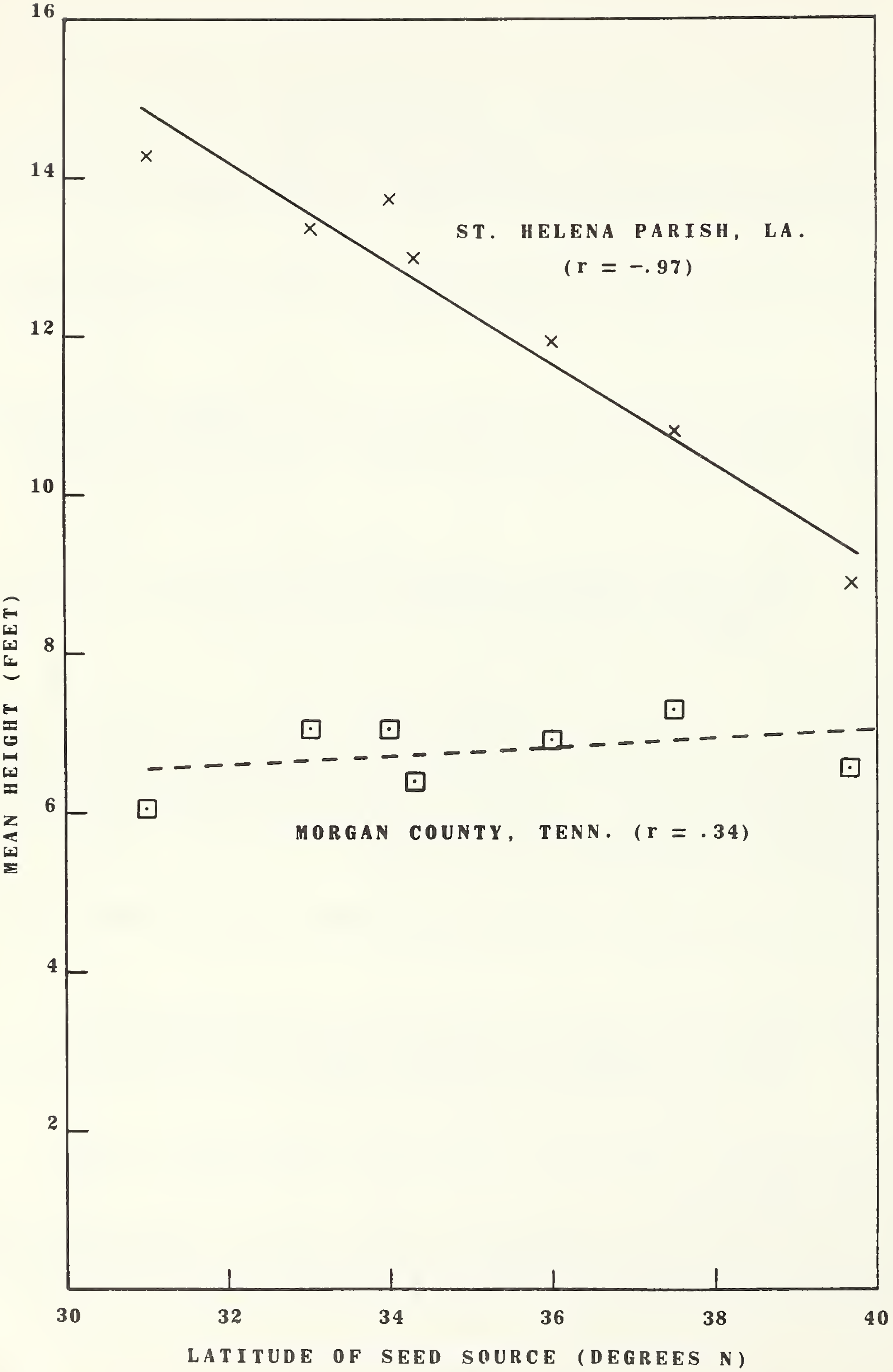


Figure 9.--Mean heights of shortleaf stocks at 5 years, over latitudes of seed sources, in plantations at southern and intermediate latitudes.

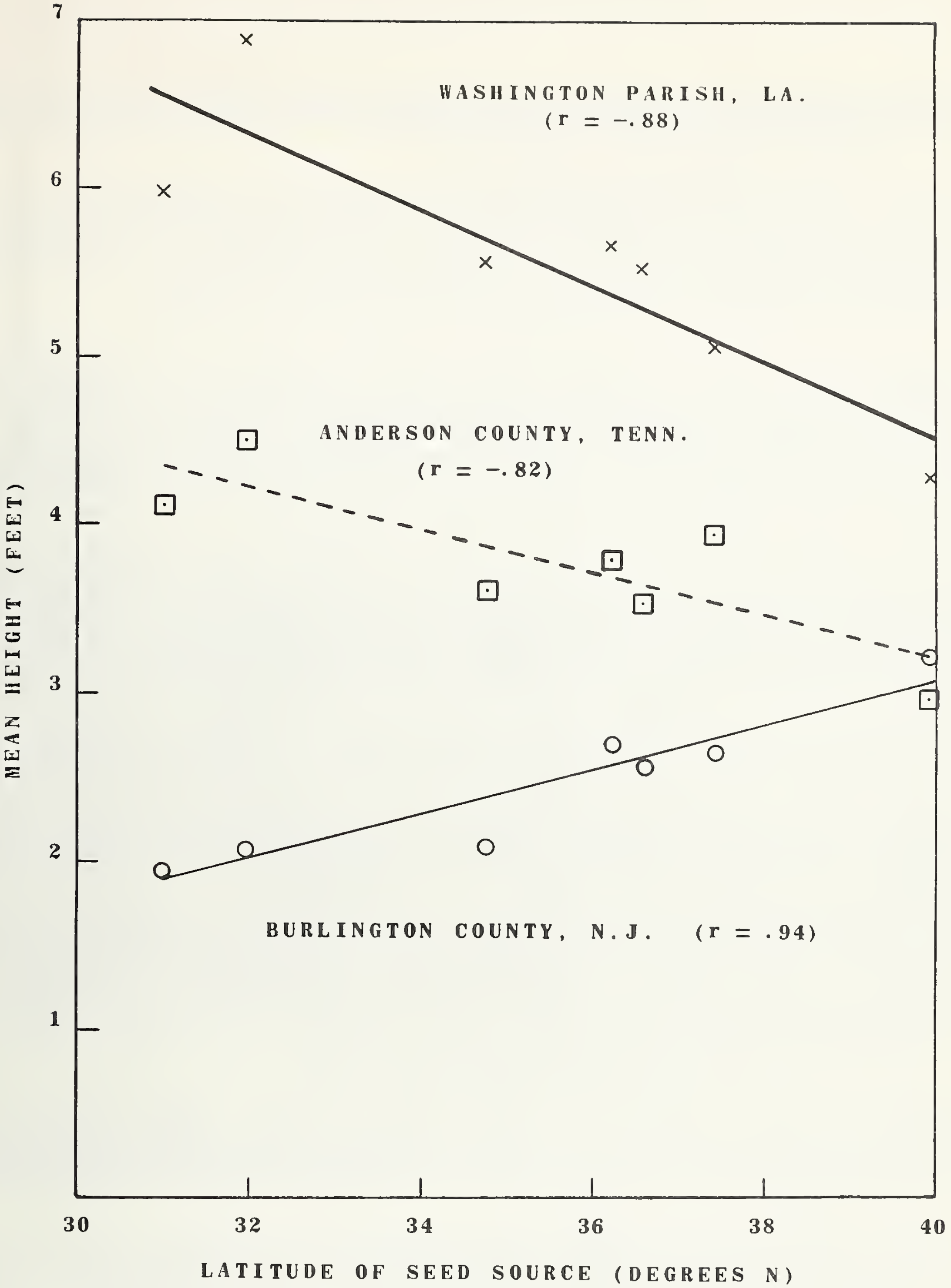


Figure 10.--Mean heights of shortleaf stocks at 3 years, over latitudes of seed sources, in plantations at northern, southern, and intermediate latitudes.

source, with a coefficient of correlation of -.88. This parallels the results of the southern plantations of loblolly and shortleaf in figures 8 and 9.

The same 7 stocks planted in Burlington County, New Jersey, at latitude 39° 36' 30" N., show an even more highly significant positive regression of 3-year height over latitude of seed source, and a coefficient of correlation of +.94. This parallels the results in the northern loblolly plantation in figure 8.

In figure 10, the curve for the Anderson County plantation alone, at the intermediate latitude of 36° 13' N., fails to parallel the corresponding Morgan County, Tennessee, curve in figure 9. In the Anderson County curve the slope is negative instead of positive and highly significant instead of non-significant. Its coefficient of correlation is -.82, as against only +.34 for Morgan County. Part of the discrepancy may be attributable to the nearly 400-foot lower elevation and probably higher temperatures of the Anderson County site.

To sum up, figures 8 through 10 show in general that, when northern and southern stocks are planted together, the southern ones excel significantly in height growth if the plantation is in a southern locality, and the northern ones if it is in a northern locality. At intermediate latitudes the differences in height growth may be less significant or nonsignificant.

These crisscrossing regression curves derived from similar or identical stocks in matched plantations at different latitudes suggest that the stocks represent points along a cline or a series of similar clines. The data show that up to 5 years, at least, the clinal relationship to latitude tends to be highly significant. The joint correlations of latitude, temperatures, and day-length are, of course, too obvious to require discussion.

The variation of height growth with latitude of seed source and of plantation is not, however, the only type of clinal variation evident from the first 5 years of the Southwide Study. The pattern of susceptibility of loblolly pine to southern fusiform rust, already mentioned under Occurrence of Significant Variation, represents a very different relationship.

At the Fifth Southern Conference in Raleigh 2 years ago, Henry (1959) reported maximum rates of rust infection on loblolly stocks from sources in and near Georgia, and lower rates on stocks from sources farther west and north.

Loblolly Series 2 consists of 9 sources from longitudes 77° 00' to 93° 00' W., and from latitudes on, and in one instance south of, the 62° - 63° F. mean annual isotherms. Figure 11 shows the regressions of mean rust infection percent at 5 years, over longitude of seed source, in plantations of this series in Craven County, North Carolina, and in Washington Parish, Louisiana.

Figure 11.-- Fusiform rust infection of loblolly at 5 years, over longitude of seed source, in western and eastern plantations.

The Craven County plantation is the easternmost in Series 2. It is at longitude 77° 00' W., in an area of relatively low incidence of rust. The curve of infection percent over longitude of seed source has a highly significant negative slope, and the coefficient of correlation is -.93.

The Washington Parish plantation is at longitude 89° 57' W., near the western end of the transect represented by Loblolly Series 2, in an area where the incidence of rush is high. The first-degree curve of infection-percent over longitude for this plantation falls just short of significance at the 5-percent level--a second-degree curve would give a closer fit--and has a coefficient of correlation of only -.62. The slope is nevertheless negative, like that of the Craven County curve. The curves for other Series-2 plantations at intermediate longitudes also have negative slopes.

The clinal relationship shown by these consistently negative regressions of infection percent over longitude of seed source is entirely different from that of the 5- or 3-year heights over latitude, in which planting at the opposite end of the transect reverses the slope of the curve. The consistently lower rust suspectibility of stock of western sources, regardless of where planted, is the main reason for recommending that non-local loblolly seed be obtained west rather than east of the planting locality.

Summary and Tentative Conclusions

The relationships so far worked out from the 5- and 3-year reexaminations of the Southwide Pine Seed Source Study may be summarized as follows:

> Although slash pine (Pinus elliottii elliottii) is represented by the fewest seed sources and plantations, numerous variations in both survival and height, significant at the 5- or 1-percent level, had developed at 5 years. With very few exceptions, however, the significant variation

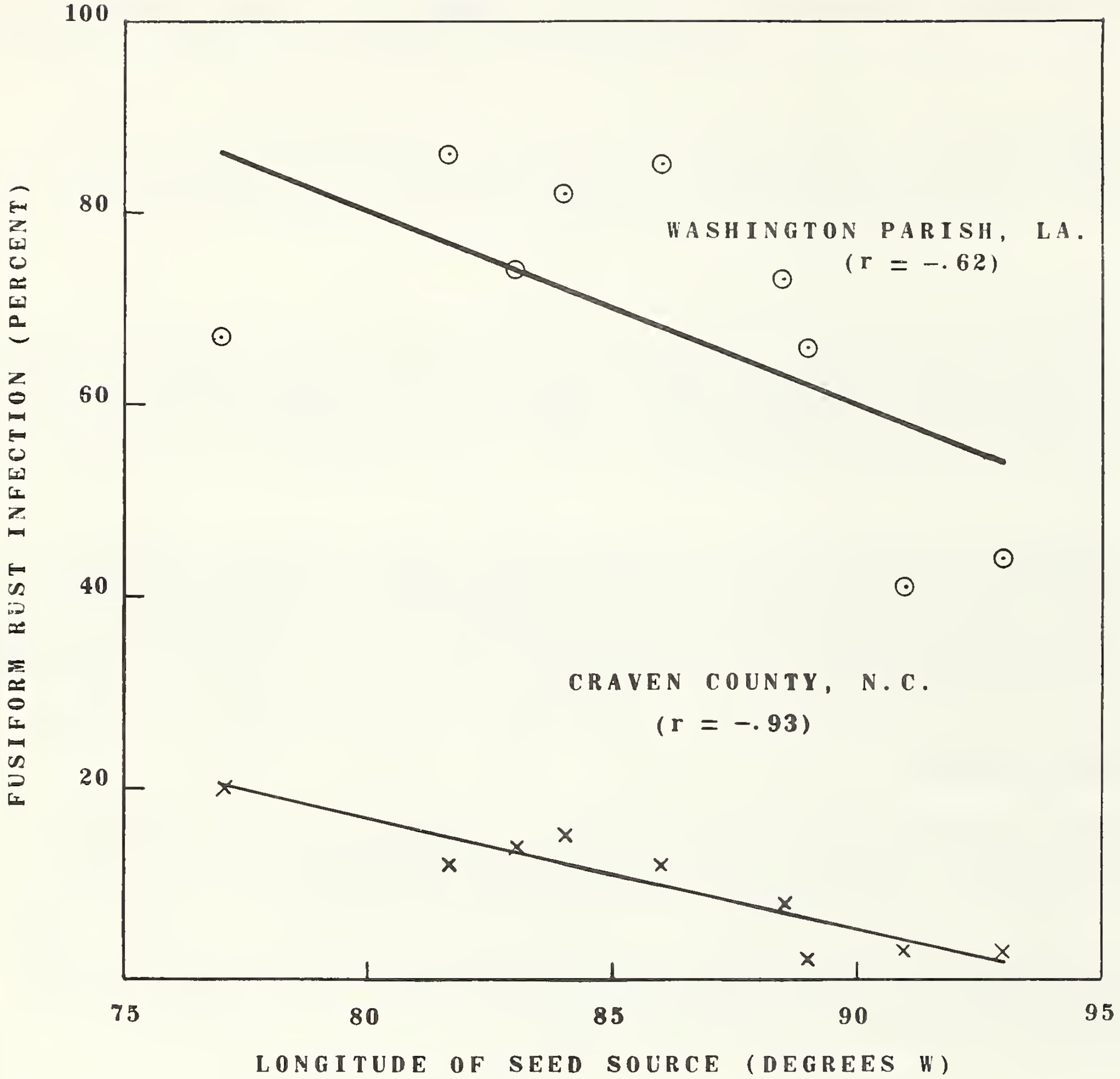


Figure 11.--Fusiform rust infection of loblolly at 5 years, over longitude of seed source, in western and eastern plantations.

was attributable to a single source, the seed from which is suspected of contamination with a recognized botanical variety, P. elliottii densa. If this one source is discounted, much less racial variation is evident in slash pine than in the other 3 species studied.

In longleaf pine, both at 5 years in the older plantations and at 3 years in the younger ones, fully as much variation in survival and height, significant at the 5- or 1-percent level, occurred among sources lying in an east-and-west direction as among those lying north and south. Variation among north-south sources was nevertheless very high in some instances. The results with longleaf must be accepted with caution because nursery conditions influenced survival in some of the older plantations, and because height relationships are unstable in longleaf up to age 5.

In loblolly pine at 5 years, and in separate plantings of shortleaf pine at 5 and 3 years, significant variations in both survival and height occurred far more frequently among stocks representing north-and-south transects of the species' ranges than among those representing east-and-west transects.

Stock from seed 'local' to the planting site was by no means always the best, or even always above the average of all stocks in the individual plantation. In a few plantations the local stock was the poorest in survival, growth, or both.

In longleaf, loblolly, and shortleaf, the design of the study permits comparison of local stocks with a limited number of other stocks planted throughout the species' ranges. In survival and height combined, local stocks compared favorably with most of these other stocks. Local longleaf stocks compared least favorably, and in each of the 3 species at least 1 other stock tended to excel local stock, in both survival and height, wherever planted.

In longleaf, loblolly, and shortleaf alike, there was a conspicuous tendency for certain individual, widely planted stocks to excel local stocks in survival but not in height, and of others to excel them in height but not in survival. In general, stocks surviving better but growing less well than local stocks represented the western parts of the species' ranges, and stocks outgrowing the local stocks but surviving less well were from southern, southeastern, or eastern sources.

> A clinal relationship of height growth to latitude proved common to loblolly at 5 years and to separate plantings of shortleaf at 5 and 3 years. When like sets of stocks were compared, curves of height over latitude of seed source had nearly significant to highly significant negative slopes in southern plantations and highly significant positive slopes in northern plantations. In plantations at intermediate latitudes the slopes were variable in direction, and less significant or non-significant. The dominant characteristic of this clinal relationship is the reversal of the slope of the curve when planting of the same stocks is replicated at the opposite end of the species' north-and-south range.
>
> In its susceptibility to southern fusiform rust, loblolly pine from the central and southern parts of its range showed a clinal relationship to longitude of seed source. This relationship differs strikingly from that of height growth to latitude, in that curves do not reverse direction of slope with change of planting location. The curves of rust infection percent at 5 years over longitude of seed source are negative in slope in plantations near both east and west sides of the species' range, and in those at intermediate points.

Only tentative and very general recommendations can safely be based on the study so far. The latest remeasurements are of survival and growth after only 5 years in plantation, and this period is far too short to permit final conclusions.

While the results to date do not strongly reinforce the traditional recommendation to use local seed, they do substantiate it to some extent. They certainly do not justify preferring seed of specific non-local sources to local seed.

With loblolly and shortleaf in particular, and to a certain extent with longleaf, the findings indicate that when local seed is not available, substitues should be obtained east or west of the planting locality, rather than north or south of it. In the central and southern part of the loblolly pine range, the pattern of fusiform rust susceptibility indicates that it is safer to go west than east for loblolly seed.

Literature Cited

Henry, B. W.
1959. Diseases and insects in the Southwide Pine Seed Source Study plantations during the first five years. Proc. Fifth South. Forest Tree Improvement Conf., pp. 12-17.

Wakeley, Philip C.
1959. Five-year results of the Southwide Pine Seed Source Study. Proc. Fifth South. Forest Tree Improvement Conf., pp. 5-11.

Weidman, R. H.
1939. Evidences of racial influence in a 25-year test of ponderosa pine. Jour. Agr. Res 59: 855-887, illus.

VARIATION PATTERNS IN NATURAL STANDS OF LOBLOLLY PINE[1]

by

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Very few studies have been made to determine the natural variation of different species of the genus Pinus. But by sampling natural populations of some pine species it has become increasingly evident that the varietal limits of the species are very broad.

A very complete study of natural variation in lodgepole pine has recently been completed by Critchfield (1957). Based on four principal morphological characteristics (resin canal number, leaf width, cone density, and cone angle) he was able to point out that not only were four subspecies present, but these populations were connected by very pronounced geographic gradients. Although the morphological characteristics in general were unique in their variation patterns, they all had in common an elevational component of varying importance. Latitude, on the other hand, did not show a clear-cut association with any single morphological characteristic. Since elevational gradients, unlike latitudinal gradients, are closely reflected by differences in the moisture climate in much of western North America, Critchfield interpreted the gradual changes in morphology to be the result of natural selection of trees adapted to xeric and mesic environments.

Rudolf *et al.* (1957) studied the natural variation of Jack pine in Minnesota and found major variations in characteristics of the cones, stem and crown form, branching habit, and disease and insect resistance. Evidence was found to support the hypothesis that the closed or "serotinous" cone character shows a clinal change from predominantly closed-cone types in the northeast to open-cone types if the southern part of the range.

Coulter pine (*P. coulteri*) has been studied by Zobel (1952) and Fielding[2]. Zobel found that despite the varied ecological and geographical conditions which prevailed in nine isolated populations, most of the characteristics which were examined showed a remarkable similarity. Fielding did not find any differences in seed coat color between different populations, but he did find great differences in cone shapes between two locations. Fielding (1953) also studied the variation in Monterey pine (P. radiata); a species which only embraces three small forests along the coast of California and a grove of trees on Guadalupe Island. Distinct differences between area in cone and seed size, seed color, and needles per fascicle were present.

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[1] Data for this paper are taken from a Ph. D. dissertation submitted to North Carolina State College by the author.

[2] Unpublished notes.

In sand pine (P. clausa) two races are present; one has closed cones, the other open cones (Little and Dorman 1952). However, no other morphological differences were found to exist between the two forms. In the other southern pines evidently no serious attempt has been made to investigate such morphological characteristics in natural populations.

Only one phase of variation has been intensively studied; the variation in specific gravity and tracheid length. Mitchell and Wheeler (1959) determined specific gravity variation for the major southern pines, and concluded that loblolly pine specific gravity showed a good relationship with the warm-season rainfall. They found that this resulted in a broadly diagonal effect of increasing specific gravity from the north-western to the southeastern part of Mississippi. Zobel and McElwee (1958) analyzed wood samples from a large number of trees from the eastern part of the loblolly range; their data indicated that a trend was present for lower specific gravity in the westward direction. Kramer (1957) found large variation among trees in tracheid length. This was confirmed by zobel et al. (1960) who also discovered that relatively large and statistically significant differences were present between different physiographic areas for this characteristic. A rather gradual increase in tracheid length was apparent in the north-south direction. The geographic distribution of trees with certain gravity characteristics was still more striking; the lowest specific gravities are found at the north and northwest extremes (Delaware and Tennessee), the piedmont has intermediate values, and the coastal plain of Georgia and the Carolinas belongs to the high density group.

Material and Methods

Collections were made in the fall of 1958 through the cooperation of thirteen different organizations. The location of the eighteen areas which were included in this study, the names of the cooperators, and some physiographical and climatological data are listed in Table 1. Figure 1 shows the distribution of the plots within the natural range of loblolly pine.

Table 1. Location and Description of Sampling Areas

Area No.	Location	Latitude North	Longitude West	Collector
1	Bastrop, Tex.	30	97	C. L. Brown, Texas Forest Service
2	Rusk, Tex.	32	95	C. L. Brown, Texas Forest Service
3	Hornbeck, La.	32	93	T. E. Campbell, A. J. Hodges Ind.
4.	Walker, La.	31	91	G. P. Finger, Gaylord Cont. Corp.
5	Crossett, Ark.	33	92	H. C. Grigsby, South. For.Exp.Sta.
6	Woodville, Miss.	32	91	B.W. Henry, South.For.Exp.Sta.
7	Tishomingo, Miss.	35	88	J. H. Hill, Hiwassee Land Company
8	Cullman, Ala.	34	87	J. H. Hill, Hiwassee Land Company
9	Opelika, Ala.	33	86	G. I. Garin, Alabama Polyt. Inst.
10	Griffin, Ga.	33	84	J. C. Barber, Southeastern For. Exp.Sta.
11	Bainbridge, Ga.	31	84	F.C. Cech, International Paper Comp.
12	Ocala, Fla.	29	82	T. O. Perry, Univ. of Florida
13	Georgetown, S.C.	33	79	P.J. Otterbach. International Paper Comp.
14	Johnston, S.C.	34	82	D.E. Cole, Cair Woodlands Corp.
15	Jacksonville, N.C.	35	78	Author
16	Wadesboro, N.C.	35	81	Author
17	Accomac, Va.	38	76	R. L. Marler, Virginia Div. For.
18	Chilesburg, Va.	38	78	R. L. Marler, Virginia Div. For.

Table 1. Location and Description of Sampling Areas - Continued.

	Physiographic	Av.Monthly Temp. °F[a]		Frostfree [a]	Annual prec. [a]
	location	January	July	Season, Dys.	inches
1	Piedmont	50	85	270	34
2	Piedmont	48	82	248	44
3	Coastal plain	49	82	222	52
4	Coastal plain	52	81	269	59
5	Piedmont	47	82	228	49
6	Coastal plain	51	82	245	56
7	Piedmont	43	80	218	55
8	Piedmont	43	79	199	55
9	Transition zone	49	80	237	53
10.	Piedmont	47	81	240	45
11	Transition zone	52	82	264	53
12	Coastal plain	58	81	286	52
13	Coastal plain	50	80	272	48
14	Piedmont	47	81	246	45
15	Coastal plain	48	79	237	51
16	Piedmont	45	79	214	46
17	Coastal plain	38	78	220	45
18	Piedmont	38	77	200	41

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[a] Harold W. Hocker. Climatological summaries for selected stations in and near the southern pine region, 192101950. Southeastern For. Exp. Sta. Paper No. 56.

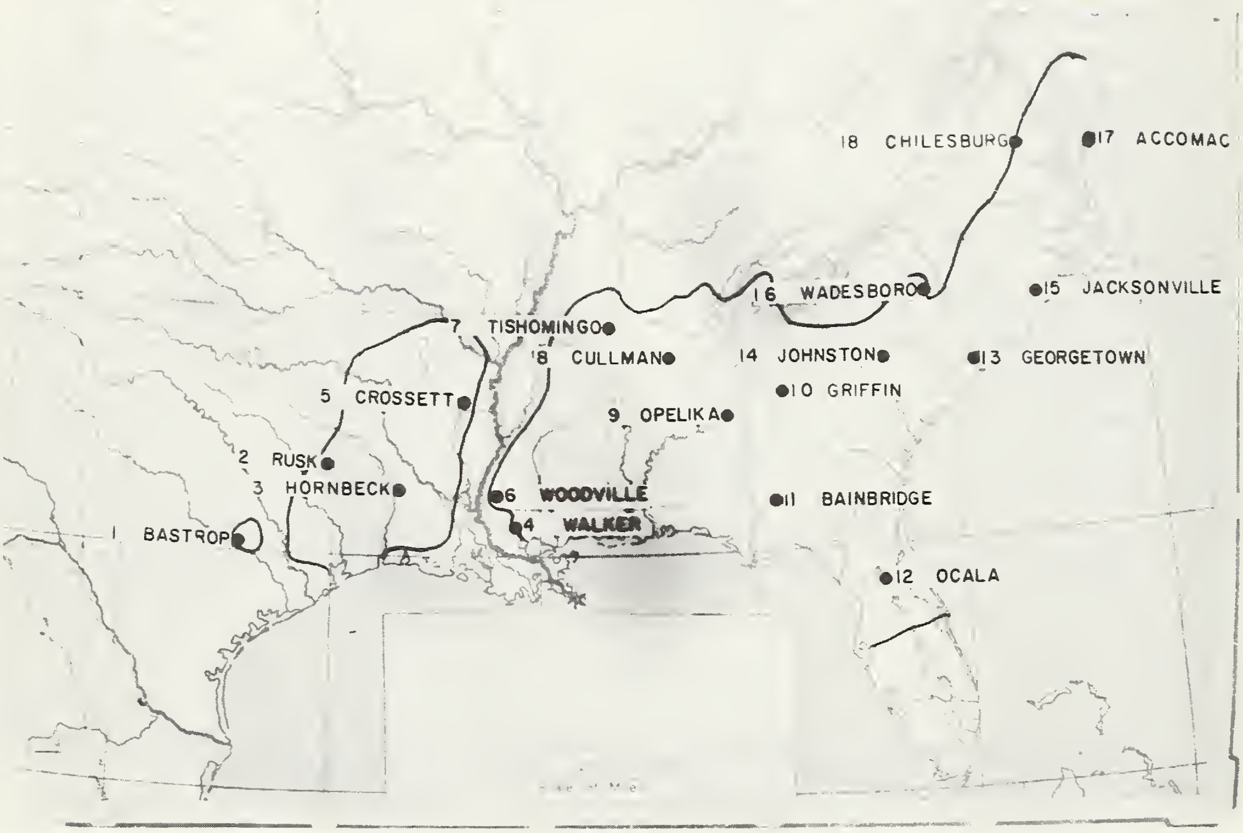


Figure 1. Loblolly Pine Range and Sample Plot Locations

Approximately twenty sound and mature cones and five twigs were collected from fifteen different trees within each area. This material was kept separate by individual trees and shipped to the writer who immediately extracted the seed and placed the twigs in cold storage.

270 trees were sampled and more than twenty thousand observations on seed, cone, and needle characteristics were obtained from this material. Only five morphological characteristics were obtained from this material. Only five morphological characteristics which showed a regional variation pattern will be discussed in some detail. These are: cone weight, seed form, seed coat thickness, number of cotyledons and stomatal frequency (stomates per linear unit).

The data were analyzed according to the nested sampling procedures (Snedecor 1956). With a large number of determinations and several levels of organization (sub-samples) the analysis of variance may become very time-consuming. The Department of Experimental Statistics at North Carolina State College developed a nested analysis program for their IBM 650 computer which was used to analyze the data in this study. The F - test was used to determine if significant differences were present among trees or locations.

Since several areas are involved in a population study the problem becomes one of multiple comparisons. A multiple range and multiple F - test designed by Duncan (1955) was used to illustrate differences present among populations.

Results

Tables 2 and 3 indicate that although a considerable amount of variation is present within trees the among tree variation is highly significant. The proportion of the total variation which is accounted for by individual trees varies from 21 percent for number of cotyledons to 63 percent for cone weight. Individual tree variation will be the basis for a large proportion of the improvement which tree breeders hope to obtain by selection of trees with desirable characteristics. The tree breeder should be encouraged by the tremendous tree to tree variation in loblolly pine, which tends to conceal differences which may be present among populations.

Of the thirteen morphological characteristics which showed highly significant differences among areas in the analysis of variance of natural populations, the majority did not show regional trends (e.g. wing length, seed length, cone length, needle length, and frequency of serrations on the needle margin). Random distribution of means may, of course, be interpreted as resulting from local environmental effects on the expression of characters.

Table 2. Analysis of Variance

Variable	Source of Variation	df	Mean Square
Seed Form	Areas	17	.043996 ***
	Trees in areas	252	.009829 ***
	Determinations	1060	.001658
Seed Coat Thickness	Areas	17	.00011944 ***
	Trees in areas	252	.00001043 ***
	Determinations	1080	.0000084
Cone Weight	Areas	17	918.95 ***
	Trees in areas	252	160.89 ***
	Determinations	1080	8.12
No. Cotyledons	Areas	17	9.09 ***
	Trees in areas	252	1.55 ***
	Determinations	1080	.61
Stomatal Frequency	Areas	17	18.93 ***
	Trees in areas	252	4.86 ***
	Determinations	1080	.94

Table 3. Components of Variance in Percent

Component	Seed Form	Seed Coat Thickness	Cone Weight
Area	12	34	20
Tree	44	46	63
Determ.	44	20	17
Total	100	100	100

	No. Cotyledons	Stomatal Frequency
Area	11	10
Tree	21	41
Determ.	66	49
Total	100	100

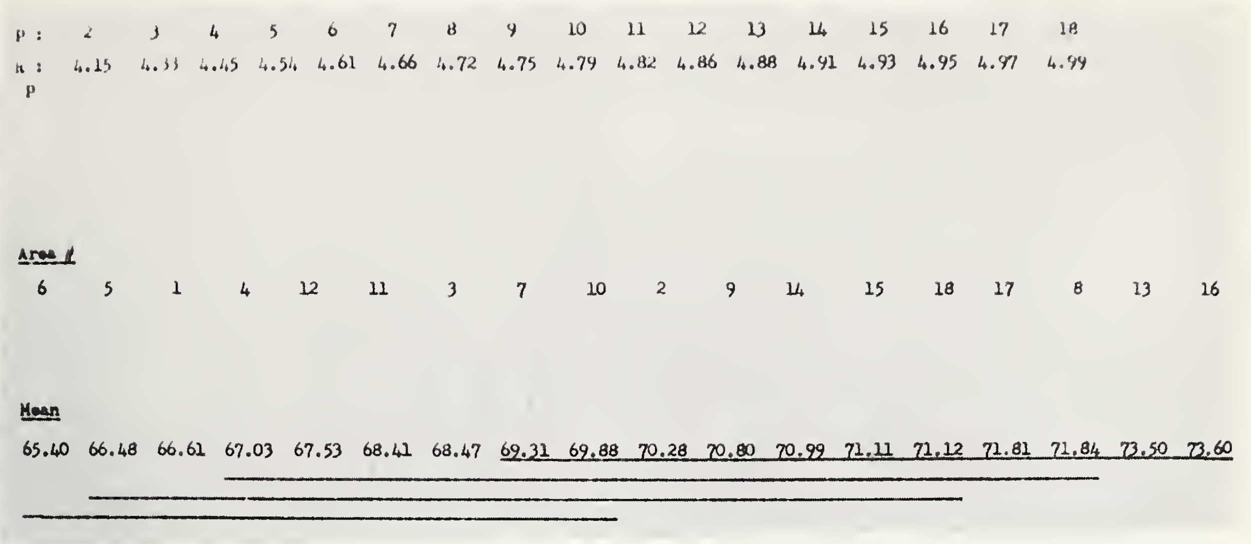
However, the possibility that genetic factors are involved cannot be disregarded. If initial population sizes were very small, Wright (1943; 1946) has pointed out that local populations may develop which are genetically distinct. "Genetic drift" may thus be a factor in differentiation of morphological characteristics in loblolly pine. Since most of the characteristics measured in the present study have no apparent selective value, although they may be linked to some physiological character, it is not probable that strong selective forces have acted on them. However, seed form, seed coat thickness, cone weight, cotyledon numbers, and stomatal frequency did show some regional trends, and it is possible that some of these characters have a selective value.

Seed Form. Seed form, expressed as seed width in percent of seed length, gives strong evidence of a regional pattern. Figure 2 shows that plot 6 to 3 have narrow seeds, plots 7 and 10 are intermediate, and the plots from 2 to 16 have a more rounded type of seeds.

This relationship is illustrated graphically in Figure 3. All the plots from the northern and eastern portion of the species range have rounded seeds; while all those from the southern and western part of the range, with the exception of plot number 2, have narrow seeds. Plot number 2 is in some disagreement with the regular pattern, but it should be kept in mind that this deviation may not be significant. From Figure 2 it is clear that plot 2 (Rusk) is not significantly different from the main group with narrow seeds even though it is barely different, at the one percent level, from the plot with the most narrow seeds (plot 6). On the other hand, around Rusk, Sonderegger (*P. taeda* x *P. palustris*) are very common and may account for the rounded seed and the large cones present in this area.

There is no indication of a sharp break in the distribution; rather there is a trend toward more rounded seed in the northeast direction. The number of plots is, however, too small to warrant a conclusion of clinal distribution. Even though it is difficult to imagine that seed form can have any adaptive value it is possible that this characteristic is associated by genetic linkage with some other characteristic, perhaps a physiological property. It is also feasible that seed form is a secondary effect of a gene or genes controlling some other morphological characteristic.

Seed Coat Thickness. Figure 4 shows that there is no indication of any discontinuity in the distribution of seed coat thickness. However, it is evident that the four plots which belong to the group with extremely thin seed coats are from the western part of the range while the ten plots with thick seed coats are from the more eastern part. This fact is illustrated in Figure 5. The number of plots is too small to prove that there is a continuous increase in seed coat thickness in the west - east direction, but the indication of a clinal pattern is quite strong.



p :	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
R_p :	4.15	4.33	4.45	4.54	4.61	4.66	4.72	4.75	4.79	4.82	4.86	4.88	4.91	4.93	4.95	4.97	4.99

Area #																	
6	5	1	4	12	11	3	7	10	2	9	14	15	18	17	8	13	16
Mean																	
65.40	66.48	66.61	67.03	67.53	68.41	68.47	69.31	69.88	70.28	70.80	70.99	71.11	71.12	71.81	71.84	73.50	73.60

Figure 2. "Duncan Test"; Seed Form, Expressed as Seed Width in Percent of Seed Length, Related to Physiographic Location.

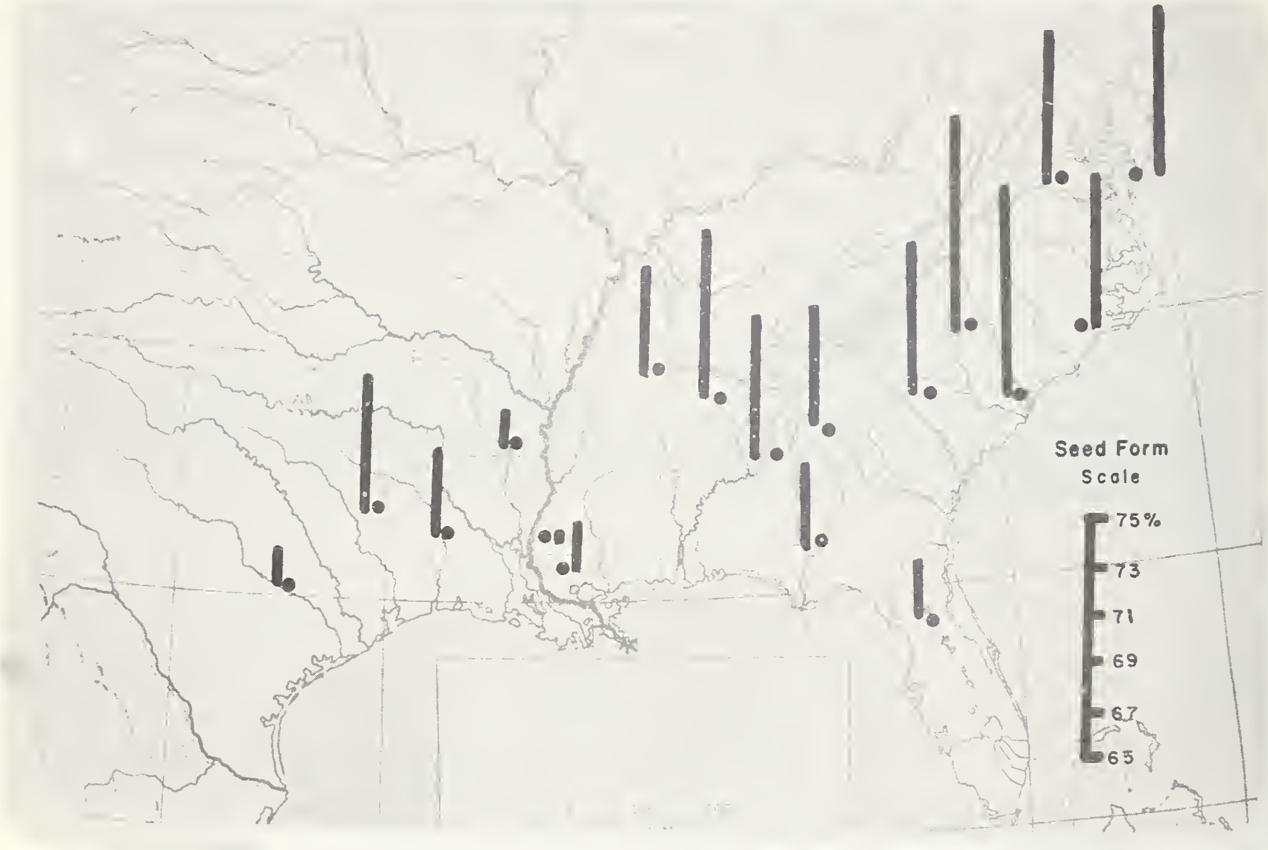
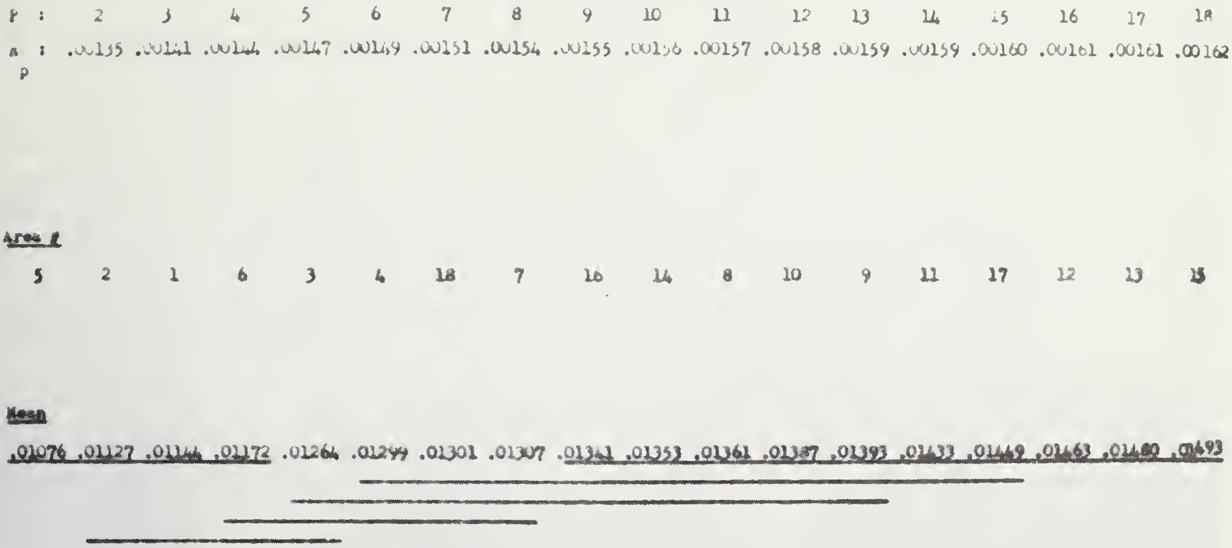


Figure 3. Means of Seed Forms, Expressed as Seed Width in Percent of Seed Length, for Regional Plots



p :	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
R_p :	.00135	.00141	.00144	.00147	.00149	.00151	.00154	.00155	.00156	.00157	.00158	.00159	.00159	.00160	.00161	.00161	.00162

Area #	5	2	1	6	3	4	18	7	16	14	8	10	9	11	17	12	13	15
Mean	.01076	.01127	.01144	.01172	.01264	.01299	.01301	.01307	.01341	.01353	.01361	.01387	.01393	.01433	.01449	.01463	.01480	.01493

Figure 4. "Duncan Test"; Seed Coat Thickness, In Fraction of an Inch, Related to Physiographic Location

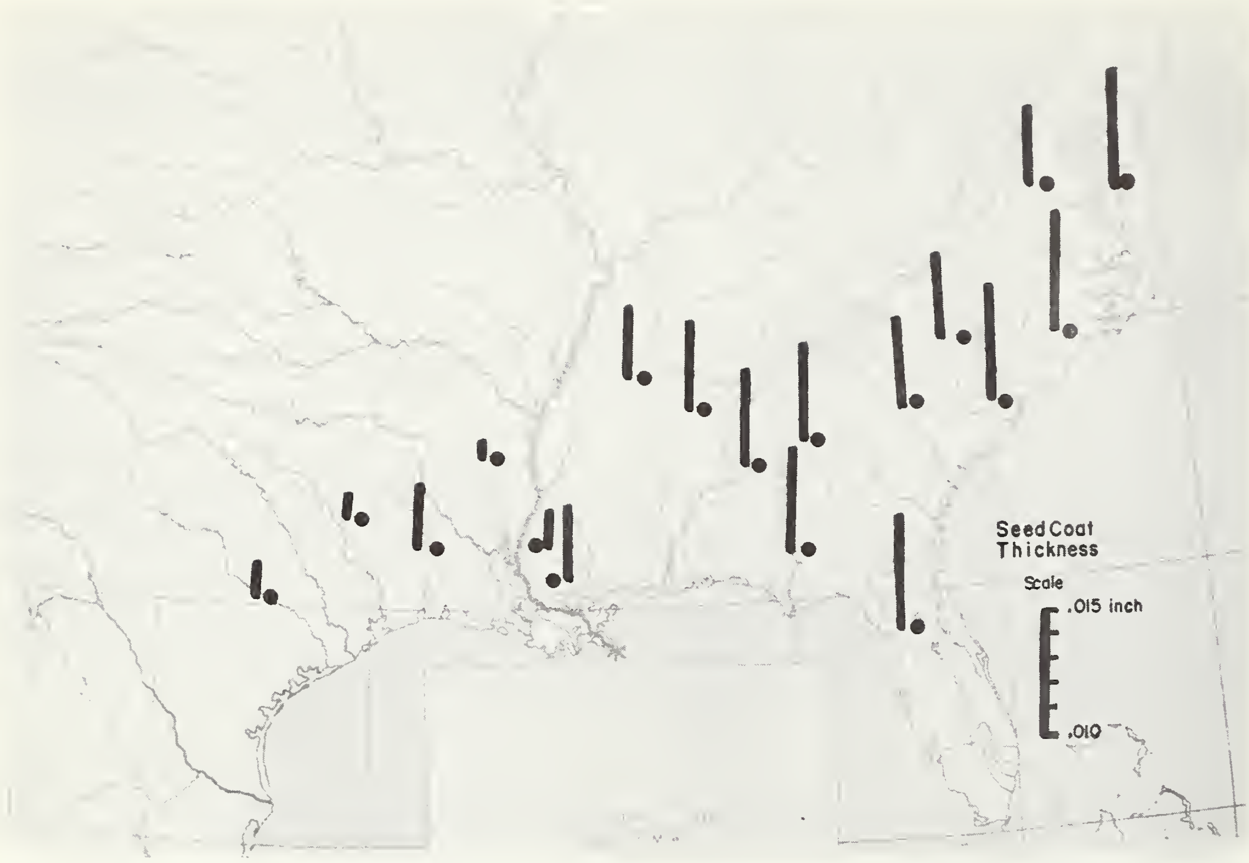


Figure 5. Means of Seed Coat Thickness for Regional Plots

Further examination of the distribution of means reveals another interesting fact; all the coastal plots have higher mean values than the inland plots. The eastern part of the range is sampled in a manner to show such relationships; each Coastal Plain plot has a corresponding plot on the Piedmont. When averages for five coastal areas are examined we find that the range of values runs from .0143 to .0149 inch, while the corresponding Piedmont values range from .0130 to .0139. Thus, there is no overlap in the distribution, and the differences between plots within the same physiographic region are negligible. It is rather tempting to conclude that two distinct types are present for this characteristic; however, such a conclusion has to be tested against other information available. From collections in North Carolina we know that there is no abrupt reduction in seed coat thickness from the coast to the western extreme of the species range.

If we define the ecotype as a race whose characteristics adapt it to a distinct habitat, there may be some objections to the use of seed coat thickness as an indicator of distinct Coastal Plain and Piedmont ecotypes. One objection is the apparently continuous or clinal distribution of the means. Since an ecological gradient is present it would, however, be expected that the corresponding means are distributed along a gradient. This means that the ecotype concept must be modified according to the scheme proposed by Huxley (1939) who suggested that an intergroup cline may be present.

In addition to this modification of the ecotype concept it would be highly desirable to show that the characteristic in question has some selective value. Since seed coat thickness distribution is highly correlated with the precipitation - evaporation ratio as developed by Transeau (1905), one working hypothesis may be that thinner seed coats allow for more rapid water uptake.

Kozlowski and Gentile (1959) found that white pine seeds with punctured seed coats had higher moiture contents than intect seeds; but the writer has not been successful in finding any reference on the effect of different thicknesses of seed coat on water absorption. A simple test in the laboratory with three lots of seeds; one with extremely thick coats, one with average, and one with very thin seed coats did not reveal any differences in ability to absorb water. After one, two, four, and eight days of soaking the moisture content on the seeds remained about constant at 30 percent, and no differences were present among seed lots. This test is by no means conclusive; when germination starts more rapid water uptake will follow and it is possible that seed coat thickness may be of importance in this part of the process.

Cone Weight. Small cones are found on trees located in the extreme southwest and southeast of the species range. The large cones are found in the central part of the species range, and the intermediates in the northeastern part. Cone size is to some degree dependent upon the environment; Ehrenbert et al. (1955) found that grafts of Scotch pine cultivated in a favorable climate produced larger and heavier cones than the mother trees. In this study, however, the largest cones were found in areas with different climatic conditions, and both Coastal Plan and Piedmont sites were capable of producing large cones.

Figure 6 indicates that only two plots, numbers 2 and 6 are in disagreement with the trend towards smaller cones in the south and west directions. Since the Duncan test revealed that plot number 6 (Woodville) is different from the other western plots, and even different from plot 4 which is located only fifty miles away, it is probable that local environmental conditions are important in determining the size of cones. It is also feasible that hybridization between loblolly pine and longleaf pine has resulted in local hybrid swarms. The introgression of shortleaf pine into loblolly could possibly explain why the cones are so small at the western extreme of the species range. In Texas[1] there is a considerable amount of natural hybridization between loblolly and shortleaf due to some overlap in time of pollen flight. Although the cooperators in this area were selecting "typical" loblolly pines for their samples it is entirely possible that some trees were contaminated with blocks of genes from shortleaf pine.

Number of Cotyledons. The Duncan test indicates that two groups with different cotyledon numbers are present. The break between these two populations is not sharp; the lower plots in the high group are not significantly different from the higher plots in the low group. The plots representing the extreme northeast, southeast, and west have fewer cotyledons than the plots from the central portion of the species range. It is also possible that all trees of the extreme south produce seeds with few cotyledons; the four southernmost locations studied have low cotyledon numbers.

Stomatal Frequency. Except for two intermediate plots there are two groups present; one small group with low stomatal frequency and one large group with high frequency. The group with low frequency is made up of the plots west of the Mississippi River with one exception, plot number 9 from the central poetion of the species range. That plot 9 is included in this group is definitely due to error in sampling. When the Opelika cone samples arrived there were no needles included and a separate collection had to be made for twigs. These twigs were evidently not collected from the top of mature trees; they were quite delicate and the needles were extremely short and light green. The writer is confident that plot 9 may be disregarded in further discussions of needle characteristics.

There is an increase in stomatal frequency in the west-east direction (Figure 7). This finding may be compared with data obtained by Mergen (1958) from a slash pine seed source test.

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[1] Personal communication with Dr. B. J. Zobel

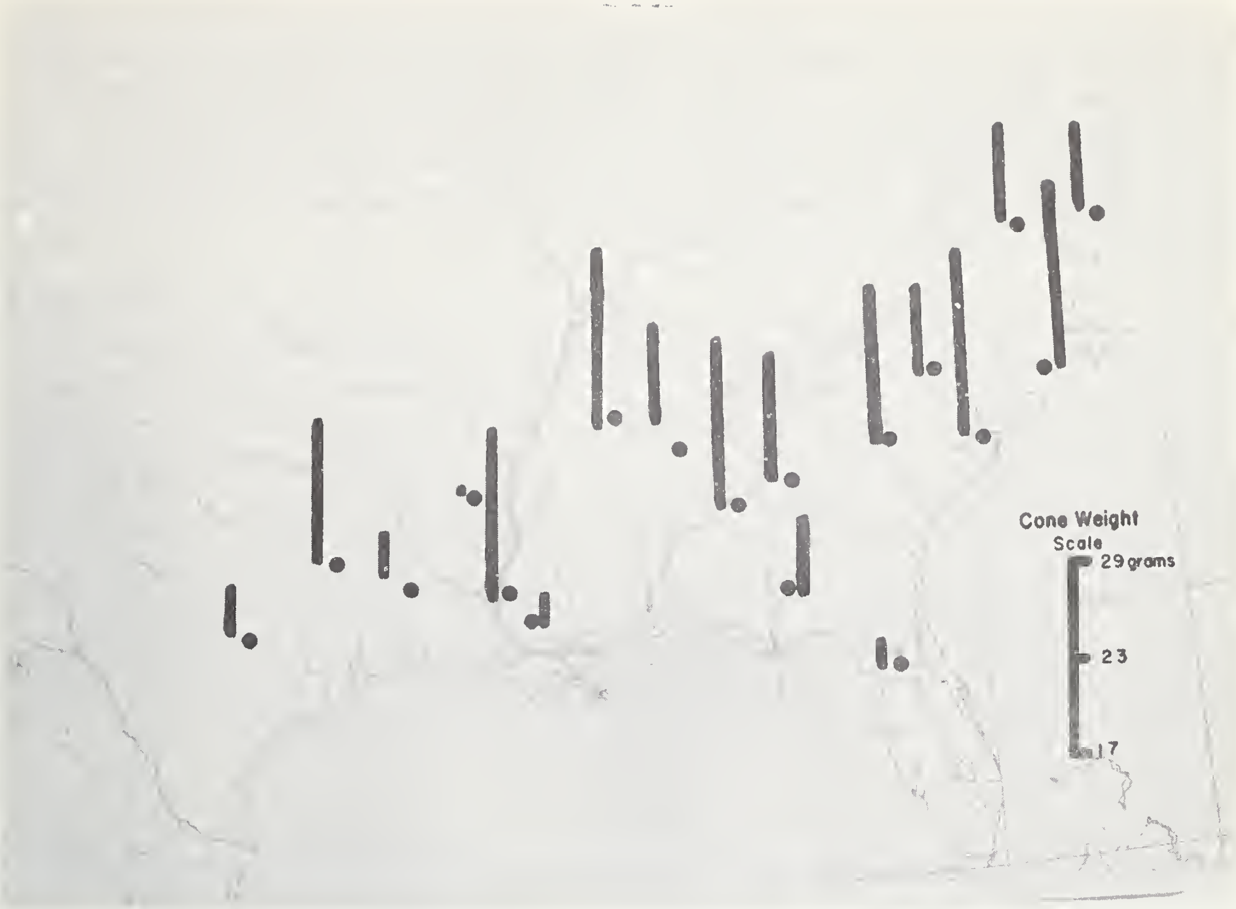

Figure 6. Means of Cone Weights for Regional Plots

When he plotted the average value for the number of stomata per millimeter over latitude, longitude, average number of days without killing frost, and the warm season precipitation, he found that the only distribution pattern that indicated a definite trend was that of a comparison with longitude. When stomatal frequency was plotted over longitude, a clinal variation pattern was revealed, with the sources from the eastern longitudes having a higher number of stomates than those from the western sources.

Thus, the general pattern of lower stomatal frequency in the west than in the east holds true for both slash pine and loblolly pine. The question is whether loblolly pine, like slash pine, has a clinal pattern. If we assume that this characteristic has developed in response to an environmental factor such as percipitation we would also expect a gradual increase in stomatal frequency with a gradual increase in precipitation. We would expect that a fewer number of stomates may be of some adaptive value under droughty conditions, and can test this hypothesis by correlating the stomatal frequency with a drought index. A drought index was constructed for each plot by using the precipitation - temperature ratio as suggested by Lang (1920). When the ratio of may to August precipitation over the average summer temperature was correlated with stomatal frequency, the _r_-value was found to be highly significant (0.666**). Therefore, there is some evidence that the number of stomates may have developed as an adaptive cline to a gradual change in moisture supply.

Summary

In this study of variation in natural stands of loblolly pine a large number of morphological characteristics were investigated. In one respect all these variables behaved alike; a large proportion of the total variation is accounted for the tree to tree variation.

Of the thirteen characteristics which showed highly significant differences among areas the majority did not show any regional trend. "Genetic drift" may thus be a factor in differentiation of morphological characteristics in loblolly pine. Seed farm, seed coat thickness, cone weight, cotyledon number, and stomata frequency gave good evidence of regional variation patterns.

The most outstanding character which varies in a clinal pattern is seed coat thickness. There is a strong increase in seed coat thickness from the western to the eastern part of the range. Similarly, all the coastal plots have higher mean values than the corresponding island plots. Thus, there is a high correlation between seed coat thickness and the precipitation - evaporation ratio.

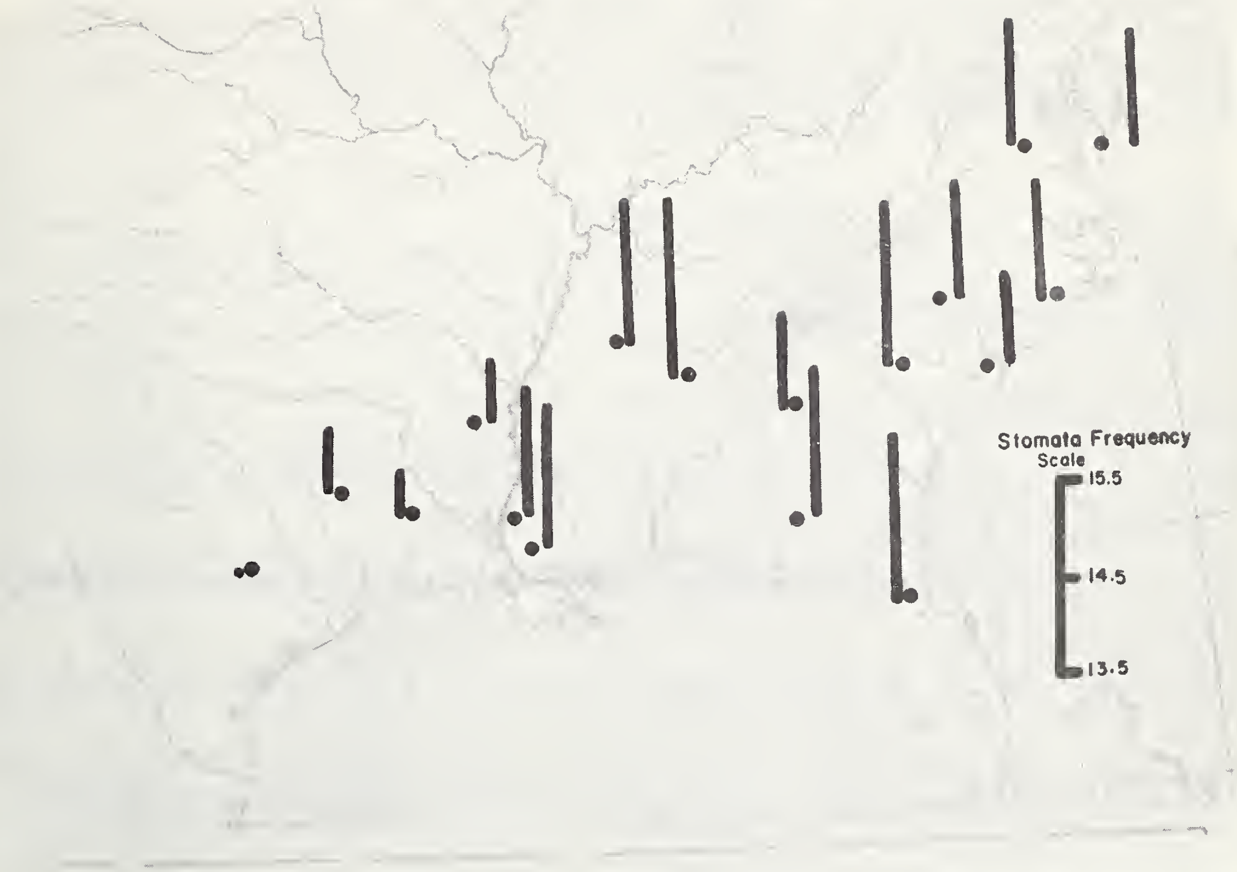

Figure 7. Means of Stomatal Frequency for Regional Plots (Plot 9, Opelika was deleted due to reasons described on page 39.)

A similar clinal distribution pattern was found for stomatal frequency. The other three characteristics, seed form, cone weight, and cotyledon number, exhibited different patterns of distribution and indicate that the different morphological characteristics have a more or less unique variation pattern. Cotyledon number, for example, was high in the central and northern part of the range, while the seedlings originating from the extreme west, south, southeast, and northeast had relatively few cotyledons.

LIST OF REFERENCES

Critchfield, W. B. 1947. Geographic variation in Pinus contorta. Maria Moors Cabot Foundation Publ. No. 3, 118 pp.

Duncan, D. B. 1955. Multiple range and multiple F tests. Biometrics 11:1-42.

Ehrenberg, C., A. Gustafsson, C. Plym Forshell, and M. Simak. 1955. Seed quality and the principles of forest genetics. Hereditas 41:291-365.

Fielding, J. M. 1953. Variations in Monterey pine. Forestry and Timber Bureau, Canberra, Bull. No. 21, 43 pp.

Huxley, J. 1939. Clines: an auxiliary method in taxonomy. Bijdr. tot de Dierk. 27:491-520.

Kozlowski, T. T. and A. C. Gentile. 1959. Influence of the seed coat on germination, water absorption, and oxygen uptake of eastern white pine seed. Forest Science 5:389-395.

Kramer, P. R. 1957. Tracheid length variation in loblolly pine. Texas Forest Service Tech. Rept. No. 10, 22 pp.

Lang, R. 1920. Verwitterung und Bodenbildung als Einfuhrung in die Bodenkunde. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart.

Little, E. L. and K. Dorman, 1952. Geographic differences in cone-opening in sand pine. Jour. of Forestry 50:204-205.

Mergen, F. 1958. Genetic variation in needle characteristics of slash pine and in some of its hybrids. Silvae Genetica 7:1-9.

Mitchell, H. L. and P. R. Wheeler, 1959. Wood quality of Mississippi's pine resources. U.S.D.A. For. Prod. Lab. Rept. No. 2143, 11 pp.

Rudolph, T. D., W. J. Libby and S. S. Pauley. 1957. Jack pine variation and distribution in Minnesota. Minn. For. Notes No. 58.

Snedecor, G. W. 1956. Statistical Methods, 5th ed. Collegiate Press, Ames, Iowa, 523 pp.

Transeau, E. N. 1905. Forest centers of eastern America. Am. Nat. 39:875-889.

Wright, S. 1943. Isolation by distance. Genetics 28:114-138.

Wright, S. 1946. Isolation by distance under diverse systems of mating. Genetics 31:39-59.

Zobel, B. J. 1952. Geographic range and intraspecific variation of Coulter pine. Madrono 11:285-316.

Zobel, B. J. and R. L. McElwee. 1958. Natural variation in wood specific gravity of loblolly pine, and an analysis of contributing factors. Tappi 41:158-161.

Zobel, B.J., E. Thorbjornsen and F. Henson, 1960. Geographic, site and individual tree variation in wood properties of loblolly pine. Silvae Genetica 9:149-158.

Ten Year Results on a Cooperative Loblolly Pine Seed Source Test

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Loblolly pine, although native only to a portion of the Tennessee Valley is being planted extensively in the region. Survival and growth of plantings made between 1939 and 1946 were so outstanding that by 1950 fifteen million loblolly pine seedlings were being produced in TVA nurseries (60 percent of total production that year). Much of the planting was on sites formerly planted to shortleaf and Virginia pine, and on most of these sites loblolly outgrew the native pines.

This extenstion naturally led to questions about the importance of seed origin on plantings outside the natural range. Therefore in 1950 the TVA Division of Forestry Relations in cooperation with five research centers of the Central, Southern, and Southeastern Forest Experiment Stations established an exploratory but extensive test of loblolly pine seed sources.

The test was designed to provide information on significant variations of plantings of different seed sources at different locations and to compare the developement of plantings at a single locality. A work plan of the test may be found in the Appendix to "Testing Tree Progeny", an early report of the Southern Tree Improvement Committee. The plan called for testing nine seed sources at eight localities. The test planting at each locality was to contain three blocks, with each source planted at random within each block.

Seedlings from a variety of geographic seed sources were being grown in TVA nurseries in 1950 and stock from nine was used to establish the test. These nine include three from the Atlantic Coastal Plains of Maryland, Virginia and South Carolina; three from the northern fringe of the species range in north Alabama, north Mississippi and Tennessee; and three more from south Alabama, south Mississippi and northwest Georgia.

The eight original planting locations are shown in figure 1. Four were made inside the range: one each by the Oxford and Birmingham Research Centers of the Southern Station, one by the Union Research Center of the Southeastern Station, and one by TVA near Guntersville Alabama. The four plantings outside the range include one by the Harrison Research Center of the Southern Station, one by the Carbondale Center of the Central States Station, and two by TVA--one at Norris, Tennessee, and one at Gilbertsville Kentucky.

Early Progress

The year of establishment coincided with the beginning of a prolonged drought in the region. A dry spell that began in late 1949 extended through three growing seasons and became critical by fall 1952. This caused extreme differences in survival and early height growth of several seed sources. Plantings of North Carolina Coastal Plain seedlings failed completely at all locations in 1950 and a South Carolina source failed in 1951. It was not until a third replanting in 1952 that a South Carolina seed source was finally established in the test. Effect of the drought was most noticeable at the Oxford, Mississippi, locality. Because of low over-all survival and complete loss of two out of three replications, this planting was abandoned after the fifth growing season.

Performance of plantings was reported after two and five years of development (1), (3). Significant differences in survival and height for both source of seed and planting locality showed up by the end of the second year and were still evident after five years. In general, inland sources survived better and grew more in height than Coastal Plain sources. On the average, north Alabama, northwest Georgia, and Tennessee sources performed best.

Ten-Year Results

Ten-year inspection of plantings in the fall and winter of 1959 included measurement of diameter growth at breast height. The average survival, height, and diameter by seed sources are showin in Table 1 and by planting locations in Table 2. Ten-year development of plantings at seven localities is summarized in Table 3.

Survival

As expected, the average ten-year survival of seed sources is not too difficult from that reported after five years. Best survival was obtained with the northwest Georgia, Tennessee and two Alabama seed sources. The superiority of inland seed sources is evident in the 75 percent average survival for inland sources as against 52 percent for Atlantic Coastal Plain seed.

Average survival of plantings inside and outside the natural range was quite similar -- 67 percent for those inside and 69 percent for those outside (Table 2).

Height

Average total height growth at ten years did not differ by seed source or region of collection (Table 1). This is in contrast to the difference in height growth that existed at five years between inland and Atlantic Coastal Plain sources. Certain height differences showed up for plantings at different localities both inside and outside the natural range. Average height growth inside and outside the range differed by only 2 feet but the difference was enough to be significant.

Two plantings outside the natural range attained heights comparable with those inside. These were the Newton County, Arkansas, and the Anderson-Union County, Tennessee, plantings where trees averaged 27 feet after ten years. Poorest height was made by the Marshall County, Kentucky; and Hardin County, Illinois, plantings where trees averaged 18 feet and 21 feet, respectively. Of all test plantings, these were the farthest north.

Among the plantings inside the range the one in Jefferson County, Alabama, attained the best height -- 29 feet. The next best planting was in Union County, South Carolina, where trees averaged 25 feet; however, this was significantly less than growth in Jefferson County, Alabama. Poorest height growth was in the Marshall County, Alabama, planting where trees averaged 22 feet.

Diameter

There was a real difference in diameter growth between seed sources at ten years. Average diameter growth ranged from 5.0 inches for the north Alabama seed source to 4.0 inches for the South Carolina source (Table 1). Trees from the north Alabama seed grew significantly better than those from south Mississippi and the three Atlantic Coastal Plain seed sources. The Tennessee source outgrew the three Atlantic Coastal Plain sources, and the Georgia, north Mississippi and south Alabama sources outgrew the Maryland and South Carolina sources. Except for the south Mississippi source, inland sources generally were superior in diameter growth to Atlantic Coastal Plain sources.

Differences in average diameter growth between plantings inside and outside the natural range are significant after ten years. Plantings inside the range averaged 5.0 inches while those outside averaged 4.4 inches. However, the best diameter growth occurred outside the range; in the Newton County, Arkansas, planting trees averaged 5.4 inches.

Growth of plantings inside the range was relatively uniform. However, of the four outside the natural range, two grew vigorously and two grew poorly. As mentioned above the Arkansas planting averaged 5.4 inches in diameter. The one in Tennessee averaged 4.8 inches. Those in Kentucky and Illinois averaged 3.4 and 3.9 inches, respectively. These last two lie the farthest outside the natural range of loblolly pine.

Individual Localities

The Marshall County, Alabama; the Newton County, Arkansas; and the Hardin County, Illinois; plantings showed significant differences in survival between sources. Significant height differences were found in plantings at Jefferson County, Alabama; Marshall County, Alabama; Union County, South Carolina; and Anderson-Union County Tennessee. Diameter growth differed significantly in the two Alabama and the east Tennessee plantings.

Distance

At five years survival was related to distance between point of seed collection and planting locality. This relationship has continued through ten years but the variation in the pattern is still too great to draw definite conclusion. While distances up to 500 miles show less variation than distances of 500 to 1,000 miles, good performance was obtained with Georgia seed as far as 820 miles from the seed source. But poor performance was exhibited by seed planted much closer to its origin.

Neither height nor diameter growth was related to distance between origin of seed and planting locality. These measures were affected only insofar as good survival generally forecasts good height and diameter growth and vice versa. Analysis of growth and survival data by plots supports this relationship.

Relative Performance of Sources and Planting Sites

A simple index was used to express the over-all relationship of survival, height and diameter with respect to seed sources (Table 1) and planting localities (Table 2). Outside the loblolly range, the Tennessee planting showed up best, with the Arkansas planting ranking close second. The poorest planting inside the range was in Marshall County, Alabama, the poorest outside at Marshall County, Kentucky.

Relation of Ten-Year Results to Earlier Findings

While final recommendations on seed sources must wait for an evaluation of wood volume and quality, ten-year data support certain inferences made after five years. General observations with respect to the better survival of inland seed sources were confirmed and sharpened. Average survival of plantings inside and outside the natural range support observations by Wiesehuegel (3) that early survival of loblolly pine outside its range is affected more by available moisture than by difference in latitude or temperature. Differences in height growth after five years were less pronounced at ten years. However, those sources that were tallest five years ago are now largest in diameter. Differences in over-all developement inside and outside the range remain the same with few exceptions. It is reassuring to know that early examination of seed source plantings can give good indications of future performance.

Only quantitative measurements were taken through the first ten years. With results on survival now fairly well clarified, subsequent inspection will be concerned with basal area, volume and quality. There will also be an opportunity to evaluate storm and ice damage. Through the first ten years no appreciable damage was reported for any of the plantings. An exception was in southern Illinois where trees from deep south seed sources sustained considerably more damage than trees from Maryland, Virginia and Tennessee.

Summary

On the basis of ten-year development the performance of nine loblolly sources in plantings inside and outside the natural range can be evaluated as follows:

1. Inland seed sources survived better than Atlantic Coastal Plain sources. Of the inland sources, northwest Georgia, north and south Alabama and Tennessee sources survived best. It would apprear that Atlantic Coastal Plain seed should not be planted outside the natural loblolly range until evidence to the contrary is forthcoming. The present tests also suggest a similar restriction for mississippi seed sources.

2. In contrast to results at five years, there is now no significant difference in height between seed sources. Loblolly pines planted inside the natural range grew 2 feet taller on the average than those planted outside the range.

3. Inland seed sources grew to larger diameters than Atlantic Coastal Plain sources. Of the inland sources, all but the south Mississippi seed source were generally superior in diameter growth. Trees planted inside the natural range averaged 0.6 inch more in diameter than those planted outside. However, the 5.4-inch average diameter growth of the Arkansas planting exceeded that of all other planting.

4. Distance between point of seed collection and planting site should not be used alone to evaluate the suitability of seed source. While there is a general decrease in survival with increase in distance, the wide variation in some sources suggests that other factors are involved. Neither height nor diameter growth was affected by increase in distance from seed source.

Literature Cited

1. Cummings, W. H. 1952. Loblolly Pine Shows Early Differences with Source of seed and Locality of Planting. Journal of Forestry 50(8): 626-627.

2. Wiesehuegel, E. G. 1952. Testing Tree Progeny. Southern Forest Tree Improvement Committee. TVA Technical Note 14. (Appendix contains work plan for this study.)

3. ________________ 1955. Loblolly Pine Geographic Seed Source Tests -- Five Year Results. Proc., Third Southern Conf. on Forest Tree Improvement, New Orleans, Louisiana, Jan. 5-6.

Table I.--Average Survival, Height, and Diameter of Ten-Year-Old Loblolly Pine by Sources of Seed

Origin of Seed	Survival percent	Height feet	Diameter inches	Performance index[b]
Atlantic Coast:				
Maryland	52	23	4.6	55
South Carolina, lot 2[c]	49	24	4.0	47
Virginia	56	24	4.6	62
Average	52	24	4.4	55
North Inland:				
Alabama	82	26	5.0	107
Mississippi	63	24	4.8	73
Tennessee	80	24	4.8	92
Average	74	24	4.9	87
South Inland:				
Alabama	81	24	4.8	93
Georgia	86	24	4.9	101
Mississippi	61	23	4.5	63
Average	76	24	4.8	88
All-average	68	24	4.7	77

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[a] Ten-year survival percentages are generally higher than reported after five years because planting in Lafayette County, Mississippi, with an initial survival of 26 percent has since been dropped.

[b] Cross product of survival percent, height in feet, and diameter in inches.

[c] Eighth year survival, total height and diameter adjusted to ten-year basis. The original planting from North Carolina seed failed and was replaced the following year by South Carolina seed lot 1, which also failed. The South Carolina seed lot 2 planting was established in winter 1951-1952.

Table 2.--Average Survival, Height and Diameter of Ten-Year-Old Loblolly Pne by Planting Locations

Planting Locations	Survival Percentage	Height Feet	Diameter Inches	Performace Index[a]
Inside Natural Range:				
Alabama, Jefferson Co.	85	29	5.0	123
Alabama, Marshall Co.	39	22	5.0	43
South Carolina, Union Co.	76	25	4.9	93
Average	67	25	5.0	84
Outside Natural Range:				
Arkansas, Newton Co.	68	27	5.4	99
Illinois, Hardin Co.	69	21	3.9	57
Kentucky, Marshall Co.	54	18	3.4	33
Tennessee, Anderson and Union Co.'s	85	27	4.8	110
Average	69	23	4.4	70
All Locations--Average	68	24	4.7	77

[a] Cross Product of survival percent, height in feet, and diameter in inches.

RACIAL VARIATION IN ROOT FORM OF LONGLEAF PINE SEEDLINGS

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The study reported here was directed at detecting geographic variation in inherent root form in the main part of the range of longleaf pine (Pinus palustris Mill.). It indicated that the roots of 1-year-old longleaf pines from seed sources in southeastern Georgia are more fibrous than those of seedlings representing sources farther west.

Of what interest could variation in root characters be to tree breeders? Laitakari (1929) reported that a fibrous root system, with 90 percent of its absorbing roots in the humus layer, resulted in fast initial growth, and Derr and Enghardt (1957) found that fibrous roots increased resistance to windthrow. Enchanced planting success is also expected of fibrous-rooted stock. Little and Somes (1951) proposed breeding for a fibrous root system. For drought areas, on the other hand, Righter and Duffield (1951) advocated hybridizing pines for taproots. In genetics research, a distinctive root habit could serve as a useful "marker" in studies of inheritance.

Has evidence of root variation in longleaf pine previously come to light? Wakeley (1953) reported that in 1928 seed collected somewhere in southern Georgia yielded seedlings strikingly more diffuserooted than those from other sources. In personal correspondence he noted the same but less striking phenomena from the Soperton, Georgia, material of the Southwide Pine Seed Source Study of 1951, and several nurserymen reported it to him for this area in the 1955 phase of the Southwide Study. Dorman noted (personal correspondence) that, at the establishment of the Southwide Study plantation at the Franklin Forest Research Center, Virginia, the Florida source had notably less root development and greater needle development than sources from other States, including Georgia.

Methods

Cones were collected in 1957 from three trees at each of the following locations: 20 locations in south Georgia at about 20-mile intervals on the periphery and through the middle of the slash-longleaf forest type; 1 in southern Mississippi; 1 at the Birmingham Research Center, Brewton, Alabama; and 1 at Hodges Gardens and Experimental Area, Many, Louisiana. The Alabama and Louisiana collections were made by cooperators. The Louisiana collection was from longleaf-like Sonderegger pines.

After being weighed, seed from each location was sown during March 1958 in three randomized 6- by 24-inch row-plots in the nursery of the Harrison Experimental Forest, in southern Mississippi. The soil was a fine sandy loam. The seedlings were thinned to 10 trees per plot, fertilized, and sprayed to control brown spot disease. In January 1959 their heights were measured to the nearest 1 mm; then they were lifted with a long-bladed shovel. Taproots were pruned to 10 inches. Green weights per plot were taken to the nearest 5 g and a single plant was selected as representative of the root form of the 10 seedlings in the plot. The nine remaining seedlings were outplanted for further study. The root systems of the selected seedlings were photographed in natural size by a shadow method on 10- by 10-inch contact paper; virtually no lateral roots extended off the paper.

On these prints were measured: (1) the total length of the lateral roots, to the nearest 1 cm; (2) the number of lateral roots per seedling; and (3) the average angle of lateral root attachment to the nearest 1 degree. In analysis, numbers of roots per seedling were transformed to log of true number, minus 1, to render distribution normal.

Results

Progenies of the parent trees growing east of a north-south line joining Laurens with Echols Counties, Georgia, had a mean number of 37 roots per plant. Progenies of parents west of this line averaged 29 roots per plant (fig. 1, table 1). The difference is highly significant.

The progenies having the greatest total root lengths (average 166 cm, as against 138 cm for all others) corresponded largely but not entirely with those having the greatest number of roots per plant (fig. 1). This fact indicates a lack of perfect coincidence between number and total length of roots. Analysis of covariance of mean total root length and mean root number led to the conclusion that significant variations existed in total root length over and above that contributed via number of roots--that is, that both number and average length of roots contributed significantly to variations in total root length. Differences among average root lengths were significant, and corresponded closely to the total root lengths adjusted by covariance.

Root angle differences were not significant, but more precise experiments might detect angle variation.

Table 1.--Root and other characteristics of sampled locations

Location or Type	Wt. per M Seeds		Seedling			Root		
		Germination	Ht.	Wt.	No.	Mean lth.	Tot. lth.	Angle
	Grams	Pct.	Mm.	Grams	Log(n) - 1	Cm	Cm	Degrees
Bainbridge, Ga.	108	67	27.7	43.4	25	7.0	122	50
Boston, Ga.	108	72	26.6	42.4	31	6.8	139	51
Valdosta, Ga.	115	83	26.8	46.8	31	7.2	149	61
Statenville, Ga.	116	67	29.4	51.8	36	6.7	156	56
Stockton, Ga.	112	79	25.9	44.6	32	8.5	172	64
Douglas, Ga.	106	64	26.9	49.3	39	6.6	164	59
Pearson, Ga.	114	79	23.5	38.4	36	6.4	150	54
Homerville, Ga.	120	72	26.0	44.6	39	6.1	150	52
Argyle, Ga.	112	82	27.0	39.6	36	6.1	138	55
Blackshear, Ga.	110	80	23.7	40.1	35	5.8	133	53
Ludowici, Ga.	109	74	28.8	45.4	37	7.4	177	56
Glennville, Ga.	118	86	24.8	39.2	37	5.7	133	54
Reidsville, Ga.	127	78	25.3	48.1	35	7.2	165	52
Soperton, Ga.	112	83	26.3	43.6	38	6.7	158	51
Milan, Ga.	105	77	24.0	35.6	31	8.1	173	55
Pitts, Ga.	109	82	24.4	34.0	33	6.9	149	58
Ashburn, Ga.	101	82	26.9	41.2	27	7.1	133	50
Sylvester, Ga.	98	75	23.6	39.6	31	6.2	130	49
Moultrie, Ga.	95	69	23.6	40.6	28	6.9	131	59
Camilla, Ga.	126	59	32.6	49.2	27	7.1	132	51
Birmingham, Ala.	116	75	26.2	42.4	31	6.2	149	61
Brewton, Ala.	98	58	27.5	39.9	31	7.2	125	58
Saucier, Miss.	112	75	27.3	39.7	29	7.4	144	53
Sonderegger (Many, La.)	108	84	28.1	35.8	24	8.0	144	55
Mean	111	75	26.4	42.3	32	6.9	146	55
Probability level	-	-	.01	.01	.01	.05	.05	NS
Standard Error	-	-	1.5	2.6	3.1	.40	12	--

Possible Underlying Relationships

Do the data reveal additional influences affecting root form?

Hypothetically, progenies might have great total root length simply because of great size, expressed as green weight. Weight of progeny was underlain by seed weight: r = +.46**. Total root length, however, proved to be only weakly correlated with either seedling weight (r = +.14) or seed weight (r ≑ +.13). Evidently great total root length was not dependent upon over-all size.

Similarly, total root lengths were not closely related to root angles. The correlation between the two is +.31, non-significant. Among the progenies from Georgia sources, the 4 with the greatest root angles were equally divided between the zones characterized by high and by low total root lengths. This suggests both that angle and total length are relatively independent of each other, and that the lifting procedure had not affected the results. If lifting had introduced a bias, roots with wide angles presumably would have suffered more breakage, which would have resulted in a negative correlation instead of the positive one observed.

Could introgression with loblolly account for the variations observed? Introgressants might be recognized by similarity to the progenies of the three longleaf-like Sondereggers included in the test, i.e., by greater height than longleaf but less green weight in the nursery. Seedlings from no other location had this combination of characters and hence there is no evidence of additional Sondereggers.

Conversely, low green weight in the absence of height growth may indicate selfing; this is a possibility because, in several locations, cone-bearing trees were widely separated. Progenies representing 6 locations showed low weight and no height growth, and 5 of the 6 localities were among those characterized by the lesser total root lengths. Two of these 5 did have high root numbers. Here, perhaps, inbreeding had reduced average root length; if so, some of the discrepancies in figure 1 may indeed be attributed to inbreeding. An alternate hypothesis is that the low weights result from inherently shorter roots irrespective of inbreeding.

Environmental Factors

It appears that one of the main bases of racial root differences is soil condition. Toumey (1929) found that the initial root systems of trees are closely correlated with the particular site conditions under which the species has evolved. Lenhart (1934) found that longleaf seedlings from a single seed source varied relatively little in foot form even when subjected to different soil and moisture conditions; his finding suggests that the results of the present study were unaffected by the particular nursery soil in which the seedlings were grown.

Of the soil factors, Turner (1936) considered moisture the most important for root growth as well as height growth of pines. However, Reed (1939) emphasized that roots and shoots of pine showed markedly different immediate response to environmental factors, particularly moisture and temperature. One of the differences is that root growth is mainly restricted to the spring and fall (Pessin, 1939). Coile (1936) showed that, in the portion of Georgia covered by the present study, slash and longleaf top growth are correlated with the rainfall of the previous summer. He theorized that "This may be due to effect on elaboration and storage of foods that are used in the rapid building of new woody tissue the following spring." Top growth is necessarily preceded by root growth, which in turn is affected by summer soil moisture. Summer droughts are specified by Toumey (1929) as conducive to the evolution of tap-rooted species.

Does the summer rainfall pattern fit the distribution of root form noted in this paper? Visher's (1954) climatic maps and those of Squillace and Kraus (1959) indicate that, in the area studied, summers and falls tend to be drier to the west than to the east and that to the west periods of relative drought occur earlier in the season.

However, lack of a completely consistent root-form gradient indicates that simple environmental relations are unlikely. Squillace and Kraus (1959) are probably correct in stating that a solution to such problems will entail a thorough regression analysis of many factors. It is time that ecologists join forces with geneticists in attacking such problems. Soil moisture contents and other factors should be sampled periodically throughout the range. Although broad soil types (U. S. Dept. Agriculture, 1938) appeared to have no relation in this study, finer subdivisions might. The vegetation of the various locations sampled should be considered; e.g. Pessin (1939) noted the drastic effect of certain grass species on soil moisture content and root growth of longleaf pine. Paleontological conditions, possible migrations of the species, and a study of adaptation to fire might offer further clarification.

Summary

Roots of longleaf pine seedlings from eastern Georgia seed appeared more fibrous than those from collections further west. The number of lateral roots was greater on seedlings from seed collected east of a line joining Laurens and Echols Counties in Georgia. Differences in this character were highly significant, and appeared to be modified less by influences such as possible inbreeding than differences in average length of roots, though significance

was shown for the latter character also. No significant differences were found in the angle of attachment of the laterals to the taproots.

It is hypothesized that the more fibrous-rooted type evolved under the typically wetter summers and falls to the east.

LITERATURE CITED

Coile, T. S. 1936. The effect of rainfall and temperature on the annual radial growth of pine in the southern United States. Ecol. Monog. 6:535-562, illus.

Derr, H. J., and Enghardt, H. 1957. Some forestry lessons from Hurricane Audrey. South. Lumberman 195(2441):142-144, illus.

Laitakari, E. 1929. The root system of pine (Pinus silvestris). A morphological investigation. Acta Forest. Fenn. 33:1-380, illus.

Lenhart, D. Y. 1934. Initial root development of longleaf pine. Jour. Forestry 32:459-461.

Little, S., and Somes, H. A. 1951. No exceptional vigor found in hybrid pines tested. U. S. Forest Serv. Northeast. Forest Expt. Sta. Res. Note 10, 4 pp.

Pessin, L.J. 1939. Root habits of longleaf pine and associated species. Ecology 20:47-57 illus.

Reed, J. F. 1939. Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. Duke Univ. School Forestry Bul. 4, 52 pp., illus.

Righter, F. I., and Duffield, J. W. 1951. Hybrids between ponderosa and Apache pine. Jour. Forestry 49:345-349, illus.

Squillace, A. E., and Kraus, J. F. 1959. Early results of a seed source study of slash pine in Georgia and Florida. Proc. Fifth South. Forest Tree Improvement Conf., pp. 21-34 illus.

Toumey, J. W. 1929. Initial root habit in American trees and its bearing on regeneration. Internatl. Cong. Plant Sci. Proc. 1:713-728.

Turner, L. M. 1936. A comparison of roots of southern shortleaf pine in three soils. Ecology 17:649-658, illus.

U. S. Department of Agriculture. 1938. Soils and men. U. S. Dept. Agr., 1232 pp. illus.

Visher, S. S. 1954. Climatic atlas of the United States. Harvard Univ. Press, 403 pp.

Wakeley, P. C. 1953. Progress in the study of pine races. South. Lumberman 187(2345): 137-140, illus.

PHYSIOLOGICAL-GENETIC VARIATION IN PLANT SPECIES

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Introduction:

Through the years there have been many studies on the kinds of physiological adaptations plant species have made to the ecological niches that exist within their range. The following citations describe the kinds of physiological-genetic adaptations that have been found in studies with tree species. The work of Pauley and Perry (1954), Irgens Moller (1958), Kriebel (1956), Olsen and Nienstaedt (1959) and many others reveal races adapted to grow at different latitudes and altitudes with genetic differences in photoperiod requirement serving to control the duration of seasonal growth. The work of Walker et al (1954), Habeck (1958), Vinogradov (1949), Fukarek (1958) reveal special adaptations to serpentine soils, limestone soils, dolomitic soils, sand-stone soils and to well-drained upland soils versus poorly drained bog soils. University of Minnesota racial studies with Jack pine reveal maritime and inland races. United States Forest Service plantings at Placerville reveal maritime and inland races of lodge pole pine. Unpublished observations by Zobel and Perry indicate that there are maritime races of slash pine and loblolly pine. Zobel's research (1957) with loblolly pine reveals drought tolerant races of loblolly pine. Scandinavian research reveals the existence of races adapted to heavy snow and ice conditions. Wang and Perry (1960) have demonstrated genetic differences in winter chilling requirement for red maple, paper birch, yellow birch, and hemlock. The studies of Wakeley (1954) reveal racial variation in disease resistance. Recent research by Steinhof (1961) reveals racial and individual variation in capacity to take up and use nutrients. These are only a few examples of the various kinds of physiological-genetic variation that have been discovered through transplanting different geographic sources of trees to a number of controlled environments. I know of no instance where proper experimentation has failed to reveal racial adaptation to the environmental factor studied. Furthermore there seems to be a parallel pattern of physiological adaptations by diverse taxonomic groups. Although broad generalizations are dangerous, one is strongly led to make the following generalization from the existing evidence:

That when and where a variation in an environmental factor exists within the range of a species, there also exists a corresponding and appropriate variation in physiological-genetic make-up of the species, and that species occupying the same geographic range frequently display a parallel pattern of physiological-genetic adaptations.

Until contrary evidence becomes available forest managers will find it wise to assume, the foregoing generalization is correct.

The following results of recent research provide added support for this generalized statement about racial variation.

While at the University of Florida Dr. Wang and I made a collection of a large number of geographic origins of loblolly pine and slash pine. This collection was divided into two lots, one subjected to a day-length equivalent to that of Gainesville, Florida. The Worchester county Maryland day-length was obtained through the use of floodlights which were adjusted at weekly intervals to duplicate within plus or minus 10 minus the day-length of Maryland. The plans in the two experimental plots were measured at weekly intervals through the periods of active growth for a duration of three years. From these data a clear picture of genetic variation in photoperiod requirement and duration of seasonal growth was obtained for both slash pine and loblolly pine. At the end of three years of growth it appears that about 30%-40% of the variation in growth within sources as well as between sources can be accounted for by differences in duration of seasonal growth, while the balance can be accounted for by differences in daily rate of growth. Individual plants from the same geographic provenance or the same mother tree that cease active height growth late one year also cease active growth late in succeeding years. Weather conditions may induce a shift in phenological activity for the local species population but the individuals of the population tend to retain the same rank of early or late cessation of active growth. As might be expected the plants from the northern-most latitudes show the greatest response to the photoperiod treatments in Gainesville, Florida. The supplemental floodlights more than quadrupled the growth of the Maryland source under Florida conditions. The photoperiod treatments, however, did not succeed in inducing the loblolly sources from Maryland to grow at a rate equivalent to the Florida source. Doubtless, temperature, soil, and biological and climatic differences other than day-length are of major importance in determining total growth.

As a part of the work at the University of Florida Dr. Wang and I conducted research on the photoperiod and winter chilling requirements of a number of species including hemlock, yellow birch, paper birch and red maple. Northern provenances of these plants did not grow well in Florida even when they were given adequate winter chilling and photoperiod treatments. This indicated that there might be genetic variation in the temperature and soil requirements of these different races. To test this hypothesis I requested a National Science Foundation Research grant to go to the California Institute of Technology where it was possible to subject different provenances of red maple and loblolly pine to controlled day and night temperature treatments. Red maple plants from northern provenances, Canada, the Lake States and New England, made their optimum growth with night temperatures between 14 and 17° C. Red maple plants from Southern provenances made their optimum growth with night temperatures in the range of 20 to 23°C. Under the controlled conditions of the Earhart Laboratory red maple plants from Vermont grew best with the day temperature between 23 and 26° C. Under the controlled conditions of the Earhart Laboratory red maple plants from Vermont grew best with the day temperature between 23 and 26° C. and were inhibited by higher temperatures. Plants from the Everglades of Florida, by contrast, continued to show increased growth with increasing day temperatures up to 30° C. This was the highest experimental treatment available in the Earhart Laboratory and it was not possible to determine the optimum growth temperature requirement for Southern source of red maple. However, genetic variation in day temperature requirements is very striking. The day and night temperature requirement of the various sources of red maple correspond well with the day and night temperatures that normally prevail in the place where the collections were made. Evidently races have evolved which are adapted to the various day and night temperatures that exist in the range of red maple. The variation in growth by single plants of the same source under the same temperature regime indicates there is genetic variation within as well as between provenances.

The parallel series of experiments with two provenances of loblolly pine reveals geographic variation in the day temperatures required for optimum growth. Plants from the high altitudes of Tennessee grew better at low temperatures than plants from the hot climates of Bastrop, Texas. On the other hand, Bastrop, Texas source outgrew the Tennessee source under the higher temperature treatments of 30°. The response by two provenances of loblolly pine to controlled night temperature treatments was not interpretable and these experiments will have to be repeated.

Red maple plants of Northern provenance tend to go dormant under treatments with night temperatures above 23° C. and below 10°C. They also grew poorly and tended to go dormant under treatments with low daylight intensity. The 16-hour photoperiod used in all experiments was theoretically sufficient to permit active growth of all sources of red maple. These observations indicate that temperature and low light intensity may counteract favorable photoperiodic conditions and bring about terminal bud formation and the onset of dormancy by red maple. The red maple from Vermont grew well in the greenhouse, but grew very poorly and set terminal buds under artificial light of 1000 ft. candles or less. The Florida source of red maple grew well under both lighting conditions. This indicates that the Florida source is more tolerant to low light intensities than the Vermont source. This laboratory observation of racial variation in tolerance supports the field observations of ecologists who suggest that Southern provenances of a species are prone to be more tolerant to competition than Northern provenances.

If one examines the species range map with all of the described physiological variations in mind, it is hard to conceive two points 50 miles apart between which plants can be transported without incurring some loss of growth. Economic considerations do not permit the development of genotypes tailored to fit every ecological niche in the range of a species. Fortunately there is a large amount of variation within geographic populations and the best progenies from one locale usually will outperform the average progenies from another locale. Therefore, genetic strains can be developed that will give superior (but not optimal) performance over a fairly large geographic province. The experiences from plant breeding work with corn and other agronomic crops indicates two or three genetic strains will adequately serve the needs of a fairly large state. Of course, states like North Carolina or California will require extra attention because of the diverse environments that exist within their borders.

Literature cited:

Fukark, P. 1958. Die Standortsrassen der Schwartzfohre (Pinus nigra Arn. sens. lat.) Cbl. ges. Forstw. 75:203-207.

Habek, J. R. 1958. White Cedar Ecotypes in Wisconsin. Ecology 39:457-463-5 Refs.

Irgens-Moller, H. 1958. Genotypic variation in the time of cessation of height growth in Douglas-fir. Forest Science 4:325-330.

Kriebel, H. B. 1956. Some Analytical Techniques for Tree Race Studies. Proceedings, Society American Foresters, Memphis, Tenn., pp. 79-82.

Olson, J. S., Skarns F. W. and Nienstaedt. 1959. Eastern Hemlock seed and seedlings. Connecticut Ag. Exp. Sta. Bull. 620.

Perry, T. O. and Wang, Chi-Wu. 1960. Genetic Variation in the winter chilling requirements for date of dormancy break for Acer Rubrum. Ecology Vol. 41:785-790.

Pauley, S. S. and Perry T. O. 1954. Ecotypic variation of the photoperiodic response in Populus. Journal of Arnold Arboretum. Pages 167-188.

Steinhof, Ray J. I. 1961. An investigation of nutrient and dry matter considerations in the foliage of loblolly pine as they are related to the nutrition and growth of the trees. Student - Thesis.

Vinogradov, N. P. 1949. Mountain stands of P. sylvestris and the problem of afforesting chalk and limestone exposures. Piroda (Moska) 38:69-71.

Wakeley, P. C. 1954. Planting the Southern Pines. U. S. Forest Service - U. S. Dept. of Ag. Agriculture Mimeograph 18. Pages 14-15.

Walker, R. B., Krakenberg-R. H. Whittaker. 1954. The Ecology of serpentine soils - A symposium. Ecology 35 No. 2.

Zobel, B. J. 1957. Progeny testing for drought resistance in loblolly pine. Der Zuchter 4. 95-6.

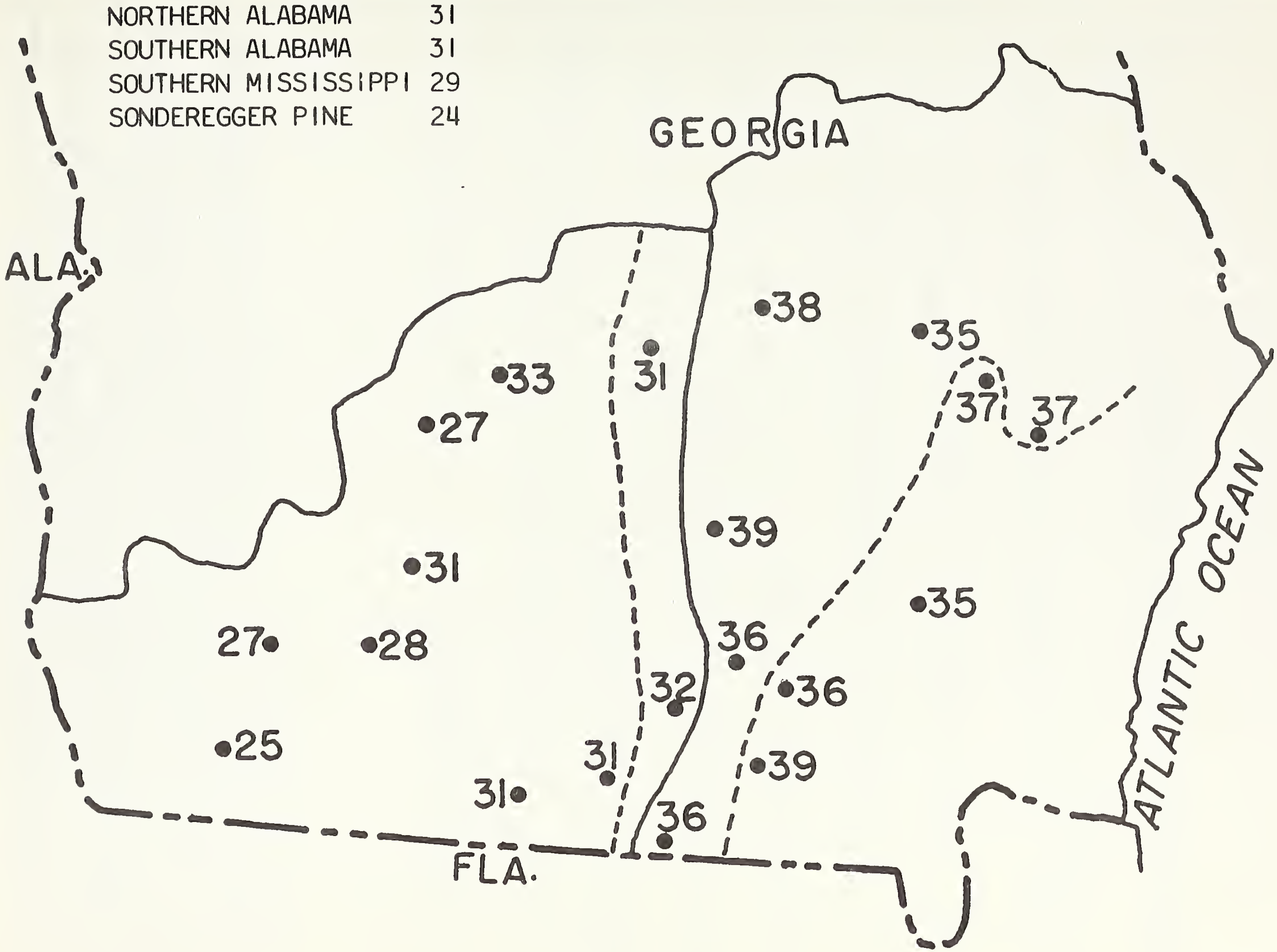

FIG. 1. NUMBER OF ROOTS PER SEEDLING FROM SAMPLED LOCATIONS. SOLID CURVED LINE DEMARKS AREA WITH HIGH VS. LOW NUMBER OF ROOTS PER PLANT, DOTTED LINES ENCLOSE LOCATIONS HAVING HIGH TOTAL ROOT LENGTH. THREE TREES WERE SAMPLED AT EACH POINT.

SELECTION AS A METHOD OF TREE BREEDING[1]

By

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One objective of tree breeding is to provide trees of better genetic quality. The speed with which the breeder can do this is a good measure of his effectiveness. Therefore, he is inclined to produce new combinations of traits with just as few manipulations as possible, regardless of whether the traits come from individual trees, races, varieties, native species, or introduced species. The tree breeder is more anxious to make use of the opportunities that present themselves, irrespective of the method of breeding or combination of methods, than to follow each classical method, such as tree introduction, selection, hybridization, or polyploid breeding, to the complete exclusion of the others. The more he can work with familiar or local trees, varieties, or species the more certain he can be that some important undesirable traits will not interfere with his plans.

The South is very fortunate in that a fairly wide variety of genetic stock is available in various species, races, and individual trees. This might be called the hope of the tree breeder and the despair of the silviculturists. It is the hope of the breeder because he can create innumerable combinations of traits for various specialized strains without having to worry much about introducing undesirable ones. It is the despair of the silviculturist because no two trees are alike.

In order to appreciate how easy it is to introduce undesirable traits along with a foreign tree species or a hybrid of a native and non-native species, just add up sometime all the factors of soil fertility, soil moisture, temperature, temperature changes, insect pests, disease pests, day length, length of growing season, windstorms and competing vegetation under which southern pines grow fast, reproduce well, and produce a large number of valuable products. A different species or species hybrid, to be more valuable, would have to excell in many traits and have no really poor traits.

Genic action can affect morphological, physiological, or chemical traits. We can't do the optimum job in single-tree selection, hybridization, or racial selection, including

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1/ Paper for presentation at the Sixth Southern Forest Tree Improvement Conference, Gainesville, Florida June 7-8, 1961.

analysis of progeny test data of any kind until we can define variation within species fairly well for all the southern tree species. It is up to the tree breeder and geneticist to make use of the skills of various specialists, such as wood technologists, pulp and paper technologists, plant plysiologists, and others to work on various traits. These people are competent in their fields of work, but need advice on how to work on the tree breeders' problems.

Forest genetics research need not be dictated by tree breeders, but it should be made to serve applied tree breeding. We have made studies in such fields as soils, botany, physiology, silvics, wood utilization, and others serve silviculture. Forest genetics should be no exception.

We should all make an effort to see that no gap exists between our basic forest genetics research and research in forest tree improvement or in applied forest tree breeding by research people or industry. Certainly it is profitable to seek out the basic laws with which we are to explain relationships, but we can exercise considerable judgment to choose the subject fields in which we want to search for "laws" and in the choice of tree species or other material with which we work. People other than foresters are concerned with the relationship between fields of research, as you will note from the following excerpt from the report of the Twentieth Century Fund by August Heckscher, Director (1961):

> "Of the responsibility of research in contribution to action I would speak in somewhat more detail. The discouraging fact seems to be that research is becoming increasingly divorced from deeds. The social sciences seem to have taken over from the natural sciences the old idea that any addition to human knowledge is of itself a boon, regardless of its seeming pertinence or relevancy. A new fact is expected to come in handy, like the missing piece of a jigsaw puzzle, when it is most needed. The trouble is, of course, that in the world as it actually exists, with its imperious necessities and its huge accumulation of books and surveys, the isolated fact is apt to remain isolated. Having been given no life or destiny by its first begetter, it is all too unlikely ever to be given life by another. It dies within its own solid covers, too remote or detached to influence the rapidly moving stream of events. Research which disavows any responsibility except that of being objective and nonutilitarian may well qualify as 'pure' but it is a kind of purity which a society--particularly a society in an age of change--can overvalue."

When a man of the stature of Glenn T. Seaborg--physicist and chancellor of the University of California--in his report as Chairman of the Panel on Basic Research and Graduate Education of the President's Science Advisory Committee (1960) makes a statement like the following

Table 3. Average Survival, Height and DBH of Ten-Year-Old Loblolly Pine by Seed Origin and Planting Locations

Origin of seed	Planted within native range[a]			Planted outside native range			
	Alabama, Jefferson County	Alabama, Marshall County	So. Carolina, Union County	Arkansas, Newton County	Illinois, Hardin County	Tennessee, Anderson & Union Counties	Kentucky, Marshall County
				Survival, percent			
Atlantic Coast:							
Maryland	77	8	73	58	53	79	16
South Carolina, lot 2[b]	79	4	58	10	73	90	31
Virginia	71	10	69	65	49	76	56
North Inland:							
Alabama	94	61	94	75	63	95	88
Mississippi	75	46	66	75	59	67	56
Tennessee	94	73	67	92	85	87	60
South Inland:							
Alabama	96	62	94	73	79	93	68
Georgia	96	67	90	96	89	94	78
Mississippi	83	19	73	72	71	81	31
				Average height, feet			
Atlantic Coast:							
Maryland	27	22	24	26	20	26	17
South Carolina, lot 2[c]	26	25	28	20	19	29	18
Virginia	31	19	25	28	20	26	20
North Inland:							
Alabama	30	23	25	28	21	30	22
Mississippi	29	24	23	28	22	27	20
Tennessee	29	20	23	27	24	27	18
South Inland:							
Alabama	29	24	24	26	20	27	20
Georgia	28	23	23	28	23	28	18
Mississippi	29	20	24	27	21	26	14
				Average DBH, inches			
Atlantic Coast:							
Maryland	4.6	5.6	4.8	5.3	3.6	4.5	3.4
South Carolina, lot 2[d]	4.0	4.8	4.8	3.5	3.1	4.4	2.9
Virginia	5.4	4.6	5.1	5.5	3.7	4.3	3.4
North Inland:							
Alabama	5.2	5.1	5.4	5.8	4.1	5.4	3.6
Mississippi	5.2	5.3	4.9	5.5	4.2	4.8	4.0
Tennessee	5.2	4.6	5.0	5.7	4.5	4.8	3.6
South Inland:							
Alabama	5.0	5.6	4.9	5.3	4.0	4.9	3.8
Georgia	5.0	5.1	4.8	6.0	4.2	5.1	4.0
Mississippi	5.2	4.8	4.8	5.7	3.8	4.7	2.2

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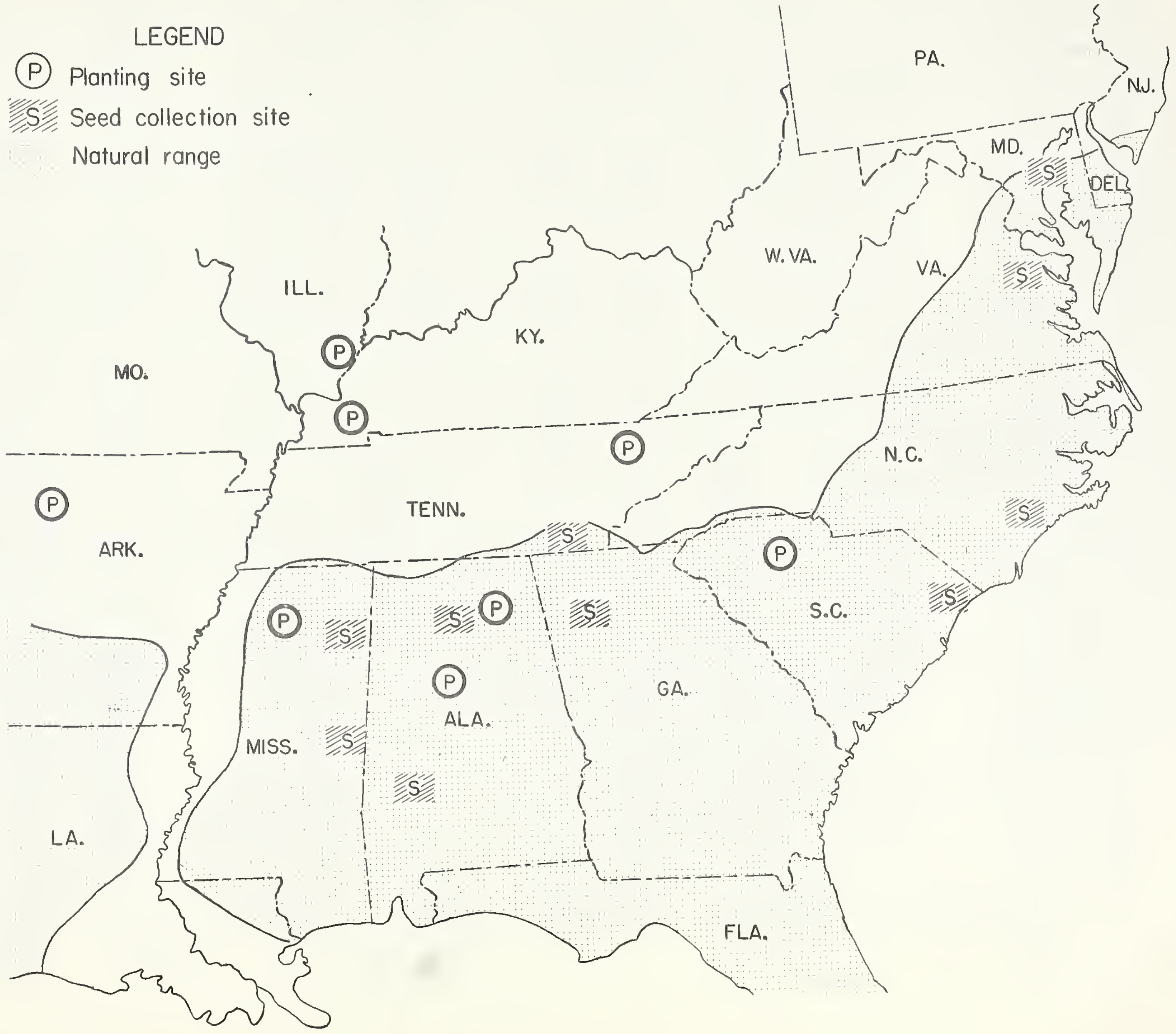
[a] Excludes the planting in Lafayette County, Mississippi, which was dropped as a failure after 5 years.

[b] Eighth year survival. The original planting from North Carolina seed failed and was replaced the following year by South Carolina seed lot 1 which also failed. The South Carolina seed lot 2 planting was established in the winter 1951-1952.

[c] Adjusted to 10-year heights; average 8-year heights were four-fifths of the values shown above.

[d] Adjusted to 10-year DBH; average 8-year diameters were four-fifths of the values shown above.

FIG. I COOPERATIVE LOBLOLLY PINE SEED SOURCE STUDY



we should pause to consider it He says, "Because basic research is aimed at understanding rather than at practical results, the layman sometimes assumes that it is entirely abstract and theoretical, and that only when it becomes a matter of industrial development does it 'come down to earth'." This is a false notion, and its falsity becomes increasingly clear with time. Indeed one striking characteristic of our scientific age has been the disappearance of the barriers between pure and applied science." Later in the same section he says, "Part of the strength of American science stems from close intellectual intercourse between basic and applied scientists. . . . . We do not believe in any artificial separation between basic and applied research or between science and engineering The fact that a scientific advance is useful does not make it unscientific."

The alternative to research in the more important fields of forest genetics with important tree species is work in unimportant fields or with unimportant species. We don't need to go overboard and everyone work on the same problems. It would be ridiculous for all of us to work on variation and inheritance in slash and loblolly pine. It would be equally ridiculous for all of us to work with holly, Chinaberry, or Arizona cypress. However, everyone should take the responsibility for directing his own work to make it effective.

With the objective of service to the tree breeders and silviculturists in mind, the work of the geneticist is often simplified because the subject fields and the species are more accurately delineated. If we accept the fact that genetics is the study of variation and inheritance, then we can pursue studies in these fields with the most important species at different locations. This may seem a narrow definition, yet it is the type emphasized in many publications. The 1936 Yearbook of Agriculture defines genetics as: "The science of heredity, variation, sex determination, and related phenomena." Crane and Lawrence (1952) in their book, "The Genetics of Garden Plants," state: "The study of uniformity and variation, of resemblances and differences between plants and the frequency in which the characters constituting these resemblances and differences appear from generation to generation is the business of the geneticist." Andrews, Warwick, and Legates Rice et al., (1957) in their book, "Breeding and Improvement of Farm Animals," say that genetics "can be defined as the science which seeks to explain the resemblances and the differences which are exhibited by related organisms." Montagu (1960) in his book, "Human Heredity," says that "genetics is the branch of biology concerned with the manner in which inherited differences and resemblances come into being between similar organisms."

Since species, racial, and individual tree variations are of such great importance to the tree breeder, strong effort should be directed toward their study. In the southern pine, particularly the major ones, species differences are fairly well defined. Studies of geographic variation are under way in the major southern pines as well as racial variation studies.

Racial variation studies in the South are, in many cases, racial selection studies also, since races of trees are grown under various conditions in which they could be planted on a commerical scale. Numerous studies of variation between individual trees have been made as well as studies of inherent variation. A great many more are needed, however, particularly of wood quality and physiological traits. If we don't select for a trait, we may in our ignorance of variation, select against it.

The one thing that held up study of within-species variation is the mistaken belief that it could be done only with sexually produced or vegetatively produced material. In other words, progeny tests or clonal tests were required. This is, of course, true if we are measuring hereditary variation; and measuring hereditary variation is very important, but it is only a part of the problem. By definition (Yearbook of Agriculture, 1936) variation is: "In biology, the occurrence of differences among individuals of the same species or variety." Rice et al., (1957) in their book on animal breeding quote this definition also. Allard (1960) in his book, "Principles of Plant Breeding," defines variation as: "The occurrence of differences among individuals due to differences in their genetic composition and/or the environment in which they were raised." Hayes, Immer, and Smith (1955) in their book, "Methods of Plant Breeding," discuss variation in connection with methods of plant breeding. So does Lerner (1958) in his book, "The Genetic Basis of Selection," Montagu (1960) defines variation as: "The occurrence of differences in characters; Discontinuous variation, graduations of differences are perceptible in the phenotype; Continuous variation, graduations of difference are imperceptible in the phenotype." Other authors use "qualitative" and "quantitative" rather than "discontinuous" or "continuous" to describe the two types of variation.

The important thing about the definitions of variation is that little if anything is said about variation being only hereditary variation or that it has to be determined by clonal or progeny tests. Allard specifically states variation is influenced by genetic composition and/or environmental factors. The basis for studying variation between plants in place is well established.

Selection and hybridization within species, as a method of tree improvement, is being used extensively with southern pines in breeding specialized varieties and in our clonal seed orchards. Based on the studies of variation and the heritability data obtained to date, some of which will be discussed in the following papers this afternoon, the rewards will be impressive. To me, this means we should hit hard by using selection and within-species hybridization as a method of breeding for still other traits, and we need to refine our techniques in breeding for traits which are now included in breeding plans. This simple breeding method is a "bird in the hand" so to speak. More elegant methods of breeding can be attempted later.

Undoubtedly, clonal and progeny tests give valuable data on variation and inheritance, and we have to have this information, but tests are slow and tests are expensive. Because they require a lot of space, rarely can they include test trees with a large number of different traits that may occur in a species. Also, to be most useful and productive, they should be based on information about variation so that the selection of traits to test is good and the design of the study is adequate, especially in regard to plot size and number of replications. In other words, to be good the progeny tests should be based on some of the data that they are now being designed to produce.

Studies of variation should be made in a logical sequence to be of the most help in applied breeding. We need them first for the economically important species at different locations over the South. We need studies of important traits of high utility and we need them for waste products, such as bark and lignin. It is common practice in research circles to make a study of a certain subject using one or two species. After the results are reported the tendency is to not follow up with more detailed studies or other species because it would seem to be repetitious. From the standpoint of forest genetics research it might be sufficient to show that trees in fairly uniform stands vary in certain traits. From the standpoint of the tree breeder, this is not adequate, because he wants to know the range of variation in each of a large number of traits, for each species, under some different environmental conditions, particularly on different sites. This is a job for research people, but, in the past, most of the data on variation and inheritance has come from applied breeding projects instead of the fundamental or basic research projects.

Studies of variation can be planned to progress in an orderly manner, increasing in cost and precision as the subject merits. Probably the most simple is to sample or measure trees under conditions where most of the factors thought to affect the trait are held as nearly constant as possible. For example, we could work with trees of the same diameter, height, and crown class in a uniformly spaced, even-aged stand on a level site where the understory is nonexistant or very uniform. It is true that this measures phenotypic variation, but it is variation where the environmental effects are as small as it is possible to make them. If no variation of economic importance is found, it certainly would not encourage anyone to test for it further in different environments or with clonal or progeny tests. If the trait does vary widely, however, additional study is warranted. This could be done with trees of different size on the same site, or then, in other studies, with trees of different sizes on different sites. If variation is still present and can't be explained by measurable environmental factors, and it occurs in economically important traits, clonal tests and others with sexually produced progeny are warranted to give information needed in seed orchard or applied breeding work. As stated earlier, these methods of studying variation put the physical effort and cost in studies where the most precision and most useful results to silviculturists and tree breeders are needed. There is little point in studying environmental effects or inheritance of traits that don't vary.

Figures on variation and inherent variation are important in many fields besides selection. Their importance in silviculture, wood technology, wood utilization, insect research, disease research, and forest survey is obvious. They are important, too, in planning interspecific and intraspecific hybridization and in analyzing and interpreting progeny test data from this work. A knowledge of variation within various species is of vital importance in carrying out geographic variation, racial variation, and racial selection studies.

Some work could be done profitably in the field of biometrics in developing methods of studying variation, and interpreting as well as reporting the results. Statistical methods should be made to serve the geneticist and the tree breeder, not the reverse. This means that methods of study used should be those that apply to southern trees and the products of southern trees, and the results should be expressed in terms that not only are understandable but useful to the tree breeder. We need to study genetic variability as well as genetic plus environmental effects. So far, silviculturists haven't been able to grow trees without an environment of some kind. Thus we must have data on the sum of both factors.

We should remember that the silviculturist does not grow only one trait of a tree or just average trees; he has to grow the whole tree and the below-average and above average trees as well, He can't tell which tree is which until they have grown awhile. Therefore, the trees that aren't average in various progeny groups or populations need to be defined as well as the average. This is useful data. Falconer (1960) in his book, "Quantitative Genetics," deals with population data of different kinds and shows how to present it with frequency distribution curves.

In the gum yield progeny test at Lake City, Florida the interim results of which were reported by Mergen and others (1955), the average gum yield of three progeny groups of plus trees after wind pollination was about 25 percent more than that of average trees. If, in a thinning, the average and below-average trees in gum yield in a population were marked, about 60 percent of the trees would come out. The gum yield of the remaining stand of trees of this size, however, would be about 75 percent, instead of only 25 percent, above that of average trees. For gum yields, the shifting in yield level of this magnitude, through silvicultural treatment, is possible because of the wide range in gum yield within progeny groups. Yield per individual tree of below 50 grams to over 450 can occur within a progeny group and is the result of genetic plus environmental factors. If the spread for a trait is less, silvicultural treatment would be less effective but still could be important. Thus, population data, trait by trait, is important for offspring of various types of mating. The man with the marking gun may become the most important "selector" of all where traits are inherited in a quantitative manner.

Industrial and public foresters, and particularly those in charge of seed orchard projects and nurseries, should keep pressure on geneticists and tree breeders to give them the kind of research data they need. Often there is a difference between what dirt foresters need and what researchers think the dirt foresters need. Most researchers are nearly human and can be reasoned with so that such contacts between people can be productive.

The silviculturist needs help with his problem of computing cost in relation to returns. Costs are difficult to determine in some types of tree breeding work, but we can probably do better than we do now. Also, the silviculturist can be reasonable in asking for cost data because the sky seems to be the limit when it comes to the way various companies are organized and the way costs and returns can be figured. Although it is difficult for researchers to figure the returns from a new method, it may be equally difficult for silviculturists to justify not making a change. For example, seed production areas obviously will not produce the ultimate in improved strains, but the geneticists and tree breeders don't know what the ultimate is nor do they know when they will produce it. In the meantime, foresters should do the best they can to obtain seed of good genetic quality. No one can say how much better is the seed from seed production areas than average or below-average seed that may be obtained from other sources, because no two seed production areas may be alike, but it is highly probable that it is better than what is being used now, and this is the important point. There is a lot of southern pine seed being used every year that doesn't come from good trees, to say nothing of the best trees. I realize there are problems, but I don't think they are all unsolvable for every individual, for every situation, in every state, for every species. The use of seed production areas is a way that selection pressure can be applied now. Seed from seed orchards of various types can be used when it becomes available. In the meantime we can do the best we can to keep seed quality high. Seed from one poor-formed southern pine tree may produce enough seed to plant 20 to 30 acres. Can tree planters afford to deliberately plant stock of poor genetic quality? The sum total of bad genetic traits plus bad environmental factors visible in some plantations of southern pine is shocking.

We should never underestimate the ability of researchers to make simple things complicated. Often this is merely the result of searching after details so that the main points become lost in mass of material, but sometimes we get carried away by the opportunity to work around the periphery of a problem rather than concentrate on the heart of it. If we continue to concentrate on studies of variation and inheritance in southern trees, use simple, effective methods to actually breed for better combinations of traits, and raise the genetic level of seed used to establish new stands, the forest geneticists and tree breeders in the South will have carried out their responsibilities well. The results of their work can then be defined in terms of trees as well as words

Literature Cited

1. Allard, R. W.
   1960. Principles of plant breeding. 485 pp., New York.

2. Crane, M. B. and Lawrence, W. J. C.
   1952. The genetics of garden plants. 4th Ed. 301 pp., London.

3. Falconer, D. S.
   1960. Introduction to quantitative genetics. 365 pp., New York.

4. Hayes, H. K., Immer, F. R., and Smith, D. C.
   1955. Methods of plant breeding, 2nd Ed. 551 pp. New York

5. Heckscher, August
   1961. Research, action, and democracy. (Excerpts from the forward "Rightly to be great." Twentieth Century Fund annual report 1959) Atlantic Econ. Rev. 11(1). 1961.

6. Lerner, I. Michael
   1958. The genetic basis of selection. 298 pp., New York.

7. Mergen, F., Hoekstra, P. E., and Echols, R. M.
   1955. Genetic control of oleoresin yield and viscosity in slash pine. Forest Sci. 1(1):19-30.

8. Montagu, Ashley
   1960. Human heredity. 364 pp., New York.

9. Rice, V. A., Andrews, F. N., Warwick, E. J., and Legates, J. E.
   1957. Breeding and improvement of farm animals, 537 pp., New York.

10. The Panel on Basic Research and Graduate Education of the President's Science Advisory Committee.
    1960. Scientific progress and the Federal Government. Science 132 (3442): 1802-1815.

11. U. S. Department of Agriculture
    1936. Yearbook of Agriculture. Agr. Yearbook 1936, 1189 pp., illus.

SOME STATISTICAL ASPECTS OF PROGENY TESTING

by
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> They went to sea in a sieve, they did.
> In a sieve, they went to sea.
> -- E. Lear

These familiar lines from a famous bit of nonsense verse seem especially appropriate, for upon reviewing the 10-year progress in methodology of progeny testing for souther species in the hope of offering some practical suggestions to progeny testers, I have the unhappy feeling of truly setting sail in a sieve on a sea of conjecture.

Ten years of progeny testing southern species have not produced as much improved methodology as we had originally hoped. Perhaps this should not be surprising. The field, after all, is relatively young, the responses are glacially slow; what appears true at one point of experience seems not necessarily true at another, and the demand for methods of high sensitivity seems always to lie beyond our immediate experience and knowledge.

If there is a fault at all, it is a persistent failure to examine the data we have in the interest of searching out information which might lead to more enlightened methods. The most encouraging fact in the 10-year history is that the whole gamut of methodology has come into sharper focus. More and more mature effort is going into answers to questions which were compromised or simply bypassed a decade ago; What size plot? What precision? Which design? We will not presume to answer these questions. We will attempt to sum up some of the experiences and preferences in the Southeastern Station's program in the hope that the recommendations they imply will be useful in the head-long program of progeny testing we foresee for commercial and industrial tree breeders.

First, we accept the minimum standards suggested by the Sub-Committee on Progeny Testing for Seed Certification as an appropriate starting point. We submit, and we believe the Sub-Committee appreciates, that the standards are only a guide for prudent governing bodies and administrators. What we offer are a few comments, and dogmas, strongly expressed, in favor of more rigorous testing and in the interest of emphasizing some of the Committee's recommendations.

I wish it were possible to make this opening point with categorical emphasis. If it were, I would offer that at this stage of our experience, we should categorically deny any progeny test not containing a statement of the least difference which, in the mind of the investigator, would be meaningful. In the early stages, when there is no knowledge of the expected differences between progeny, it is wise and profitable to indulge tests merely bracketing the range of those differences, provided, of course, that we accrue information on the kind and degree of variability which accompanies the test. This, after all, is the purpose of exploratory trial, for with some idea of the expected differences and with some knowledge of variation, the tree breeder and statistician can work together in choosing design, plot size, number of replications, and other factors which can most effectively detect the differences at any prescribed level of confidence.

But this alone is not sufficient. During exploratory trial, and certainly before definitive testing, the investigator must decide what order of difference would be meaningful. Preliminary trials may show very consistent differences, in which case the test would demonstrate high significance to the joy of the statistician. But if the differences are small, they may have little or no practical value and hence would not be meaningful to the practical tree breeder.

Note the powerful implications of a "meaningful" difference as opposed to the fashionable and often overworked "significant" difference. Whatever the degree of difference, if it is not meaningful, there would be little justification for continuing the test, no matter what its significance. On the other hand, if an observed difference is meaningful and significant, the prayers of the investigator are answered. If it is meaningful and not significant, a more comprehensive test is justified.

Among the progeny testers and geneticists of my limited acquaintance, few are willing to put precise limits on what they would consider a meaningful difference for any single trait. Fewer still would guess at the difference which by itself might be "meaningless" but which in combination with other "meaningless" differences may produce a meaningful difference for the combination. Generally, we take refuge in the accumulating evidence that differences less than ten percent are difficult to detect with our present methods.

If this problem could be inverted, and we could begin with some idea of a least meaningful difference, the net effect would be to markedly simplify initial screening of a large number of progeny, to permit more sensitive designs with fewer progeny, and generally to improve and sharpen the objectives of study. There is a most urgent need for serious consideration of what these differences should be for the thirty-odd traits under examination in various tests of southern species. I am quite aware of the staggering proportions of the task, but this Committee has not been over-awed by other equally profound problems. I offer that no other advisory body is as well equipped to suggest the guides so badly needed by research as well as by commercial and industrial tree breeders.

Categorically, we deny any design in which the number or size of plots forces blocks to be unreasonably large. This point of caution would be trite if progeny testers would observe the classic warning, but we continue to hear and read of randomized block experiments where the block ranges up to three or four acres in size. We have no great fund of evidence to demonstrate the wisdom or the fault of these designs, but there are some general guides. In theory, if a fertility gradient exists in the planting area, and if that gradient should be assigned logically to random error, the block size should decrease as the gradient increases. The intent is that differences in random fertility would be identified with blocks, and the derived error would be a valid estimate of random positional variation, and a proper error for testing differences among progeny. On the other hand, if blocks are excessively large, differences between blocks tend to vanish, but, even more important, the error tends to resemble a true site-progeny interaction rather than random variation in microsite, and hence tends to make the test insensitive.

It is difficult, if not impossible, at this point of our experience to put boundaries on block size over the range of planting sites in the South. But our experience in the piedmont of Georgia indicates that blocks approximately one acre in size are entirely too large in that area. Barber will discuss this point in some detail. In the coastal plain there is some evidence that blocks may be larger; how much larger we cannot say. The important generality is that size of block can invalidate, and for that matter often does destroy, many otherwise well designed tests, and the only plausible solution in the absence of worthy evidence is to favor small blocks.

Block size may be controlled by manipulating either the size of the plot or the number of plots it contains, or both. I will begin on a point of mild controversy and some documentation.

With few exceptions, such as limited amounts of seed from stock of exceptional value, extreme limitations in availability of land, or complete refusal of statistical inference, we categorically deny the single tree plot. In spite of its reputed efficiency, the conditions to attain that efficiency are notably absent in tests of southern species. In the first place, mortality is common, and often relatively high. Interplanting to repair damaged plots is unsuccessful because interplants remain depressed throughout at least their juvenile development. The alternative dodges of omitting plots, or using missing-plot techniques are equally unsatisfactory in that the test is always weakened, and more often utterly useless. In competition, many if not most studies are set out with the provision that competition within the plots is a necessary condition of the test. Height and diameter growth, for example, are assessed in the presence of competition from individuals of the same clone or progeny group. For this objective, the single tree plot is worthless, and our interest centers on the maximum amount of information per replicate, not per unit area.

But perhaps the most formidable argument against the single tree plot is the likelihood that the genetic portion of variation from plot to plot is non-normal. It is recognized that variation in progeny tests is of two kinds, that of the variation among trees of the same progeny, and that due to position in the plot. Much of the evidence in agriculture and forestry supports the notion that positional variation tends to be normally distributed, and that if this were the sole source of variation, single tree plots would be quite amenable to analysis of variance. But since the error of progeny tests is a combination of both genetic and positional variation, total variation may or may not be normal, depending on the relative magnitude of the two sources. With so little information on the distribution, the best gamble would seem to be a multiple tree plot, because of the property that means drawn from non-normal populations tend toward normality as sample size increases. It is, of course, anyone's guess how large a plot is required to attain normality or near-normality. We can only speculate, but it seems to be an intelligent speculation that a multiple tree plot is preferred.

Quite apart from the question of normality, optimum plot size has been examined with data from the 3-year heights of the tests at the Ida Cason Calloway Foundation in the piedmont of Georgia, and 10-year height, diameter, bark thickness, and clear length from a spacing study in slash pine of the upper coastal plain, and with data for the same traits in 2-year-old slash pine plantations in the upper coastal plain. The graphs, taken from the 10-year-old spacing study only, illustrate a point which appears in all these tests examined to date; i.e., the coefficient of variation tends to become stable in the neighborhood of 20 trees per plot for all traits observed. In itself, this is but a shred of information, but taken together with our concern with lack of homogeneity of the planting site and the likelihood of non-normal variation in very small plots, the combined evidence has led us to an arbitrary decision to use a 25-tree observation plot.

There remain, then, only the question of how many progeny can be admitted without unduly inflating block size. One-acre blocks will admit about 25 at the most. Most commercial tests will be with fewer progeny and will offer no real problem, but industrial and research programs may quite easily require space for 75 to 100 progeny or even more. Here the only alternatives seem to be:

(1) Insist upon homogeneous planting site.
(2) Ignore significance tests in favor of arbitrary and ruthless screening to reduce the number of progeny for definitive testing in a second stage.
(3) Select more sophisticated designs, such as the incomplete block.

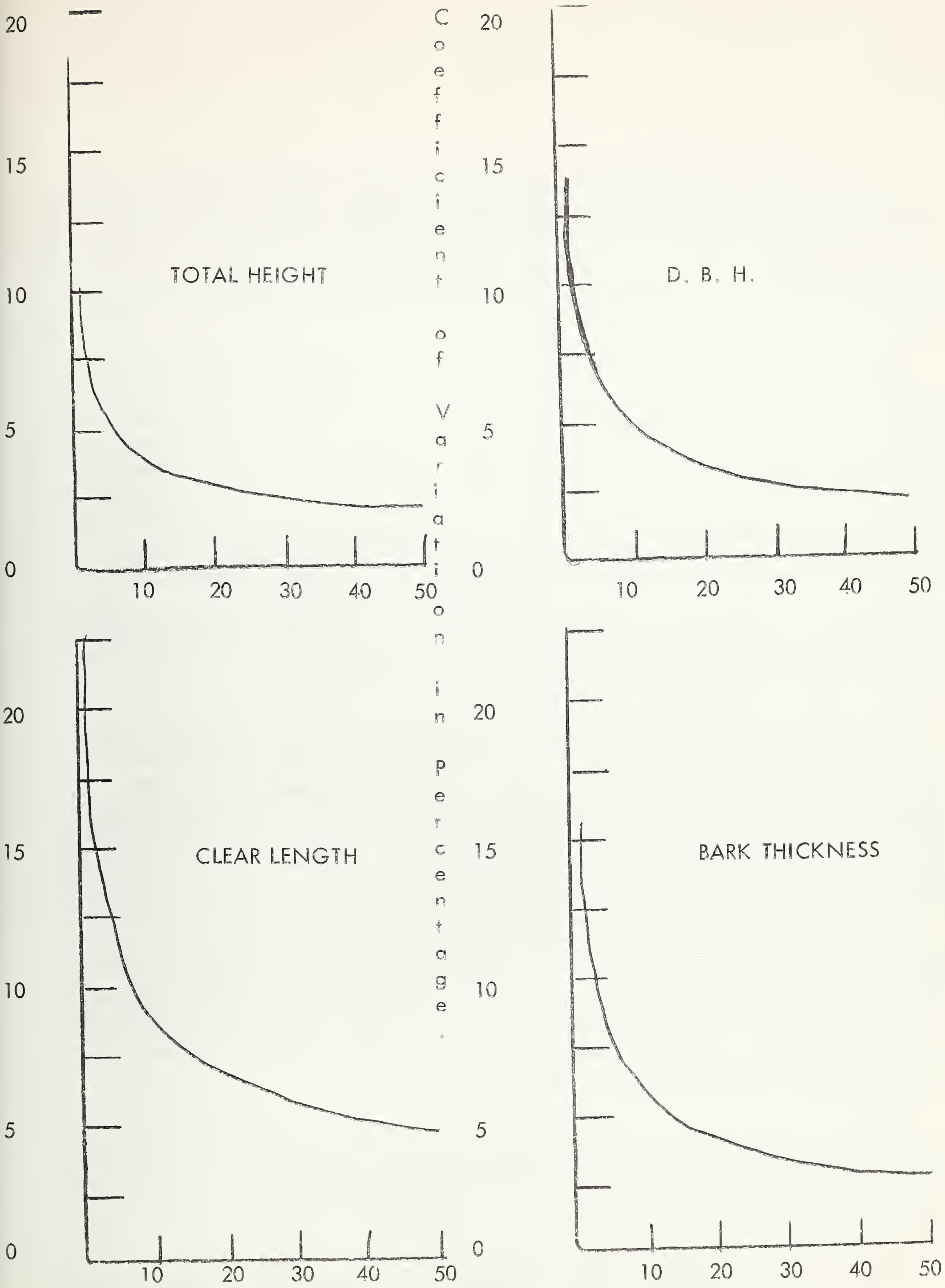

Fig 1 --Relationship of Coefficient of Variation of PlotSize in 10 Year Slash Pine.

Our decision is not yet clear, but at the moment we seem to be persuaded in favor of 2-stage testing of the plantings made during the past ten years. New plantings will be made in a series of smaller tests, each with different progeny but with one or more standard controls in each test. This will permit crude testing at the time of screening. The expected gain may be small, but in our opinion it is preferred to the imprecision of excessively large blocks on the one hand and the insecurity of the more sophisticated designs on the other.

In designing studies for the traits we have discussed and others, I assume you will be calling upon some statistician for advice. If you do, I can assure you one of his questions will be where he can get information on the variation you will contend with for the traits you will test in the area and time where you propose the test. Without this information much of his advice will be fruitless. Tree breeders and geneticists are not without data; our files and your files are full of data, most of it relevant to the point. But little of it has been published, probably because it is only of secondary interest to readers. But all of it is important to progress in the design of progeny tests; the only problem is how the information can be made available to other workers. Most of you have seen the Planning-Factors Manual issued by the Forest Service this year. It, or something like it, is one possible outlet. But whatever the outlet, I urge all of you to promptly analyze and study the data you have, and in some way make it available promptly to the rest of us. If you do, I am sure the effort will be rewarding.

One other point is worth emphasizing. Our persuasion is to refuse all second-stage progeny tests which are not replicated in both time and space. Ideally, this preference should exist for all gests, but when the number of progeny under test is large, as it frequently is in exploratory trials, the enormity of the task makes this replication utterly impossible. There is some evidence of the effect of time and space, and a considerable body of data as yet unanalyzed in our own and other files. But even without substantiating evidence, both variables should be tested; time, in the interest of assessing the response to insects, disease, drought, frost, flooding, or any other factor associated with year-to-year variation in climate; space, in the interest of assessing the response to soil, site, history, land use, or any other factor associated with place-to-place variation in fertility. And, even more important, there is every reason to examine the interactions of progeny with both time and space. The consistency with which both factors interact with species and treatment in other fields of forest research is significant evidence that the interaction may well be the most important single contribution of the tests.

There are many other points I would like to discuss with you; but in the interest of time, I have touched on only three: namely, the place of a meaningful difference, the control of block size, and the need for replication in time and space as the most important at this point in our experience.

If we have been sailing in a sieve, I would remind you that in the nonsense poem the whole nation of Jumblies took to sea in sieves after the jubilant return of the bold pioneers. Won't you join me?

INHERITANCE OF VIGOR IN SLASH PINE

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In January, 1953, a series of controlled pollinations were initiated by Dr. Tom Perry to study the transmission of vigor from parents to off-spring in slash pine. The stated objectives of this study were: (1) to demonstrate the inheritance of vigor, (2) to demonstrate the degree of genetic superiority or inferiority of the selected trees, thus giving some measure of the economic gains to be realized through forest genetics (3) to test the validity of the genetic evaluations that were made on the basis of phenotypic comparison.

To accomplish these objectives, natural slash pine stands on the Austin Cary Forest were measured for age, total height, d.b.h., and volume. A subjective estimate of competition, form, growth potential was used in making the final estimate of the vigor of individual trees. On this basis four trees of high vigor and four trees of low vigor were selected. Diallele crosses and self pollinations of each tree were planned. Unfortunately, however, there seemed to be a strong correlation between vigor and cone production and as a consequence only one low vigor tree was used as a female parent and one low vigor tree was used as a pollen source. All four of the high vigor trees were used in the cross pollinations. In addition, several trees were self-pollinated, but the selfing resulted in poor seed set and poor survival in the seed bed. Only one selfing produced adequate seedlings for an experimental design.

In 1955, seed resulting from these controlled pollinations and seed from three check sources were planted in the nursery. Resultant seedlings were outplanted in a replicated randomized block design on Austin Cary Forest in 1956. Sufficient seedlings were available to establish seven replications of four tree plots of most of the lots.

Included in this study are: three check sources--one bulk collection from the Austin Cary Forest, one from an open grown stand near the forest and one lot of state nursery seed; open pollinated progeny from two of the high vigor selections; five different high vigor crosses; one cross of low vigor trees; and self-pollinated progeny of one of the high vigor selections.

This plantation was remeasured during the summer of 1960 after the major height growth of that season had been completed, thus, this report is based on five years growth after outplanting. The height, d.b.h., and length and diameter of branches in the lower whorls were measured. This report is based upon analysis of variance of these data.

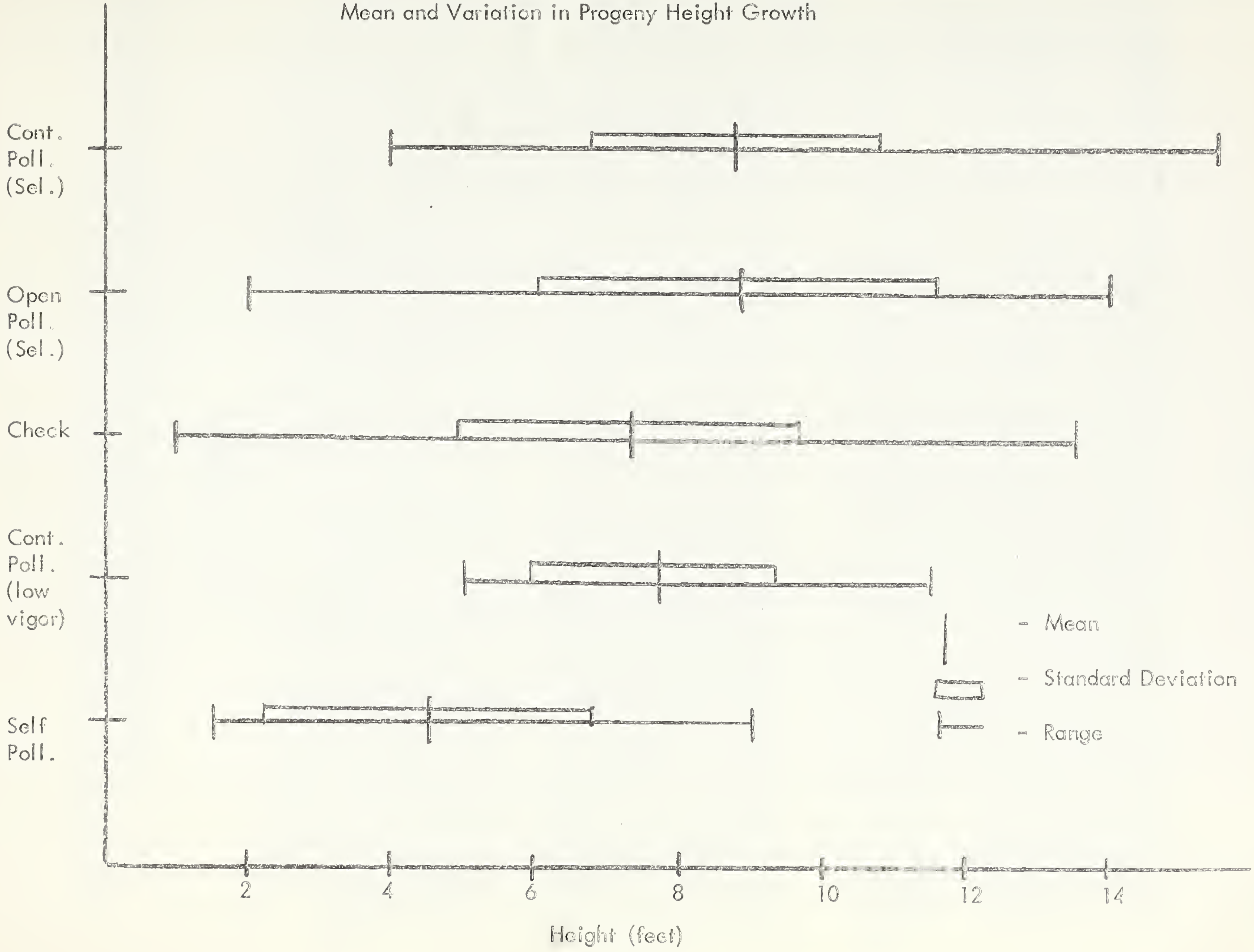
Results

The analysis of variance showed highly significant differences among the mean heights of the various sources in the study. This does not mean so much in itself considering the variety of material included in the test ranging from self-pollinations through specific crosses to wind pollinations. However, various individual and group comparisons are quite revealing. For example, the check sources as a group made significantly less height growth than either controlled or open pollinated progeny of the select trees. It should be emphasized also that these select trees are not superior trees. In Dr. Perry's own words, "Looking back after 6 years of experience in tree selections, I now see some of the high vigor selections would not be accepted by today's standards. However, some still hold good, although the form of the selected trees is poor."

The mean and variation in height growth of the several progeny groups are presented graphically in Figure 1. The average height of control-pollinated progeny of the high vigor selections was approximately 1.5 feet higher than the average height of all check sources. The progeny of the single low vigor cross had slightly greater height, but not significantly so, than the average of the check sources. Figure 1 also indicates the highly significant depression of vigor in progeny resulting from self-pollination. The progeny of the only cross between the low vigor trees was significantly different from only the very best individual cross of high vigor trees. However, the mean height of the low vigor cross approached significance at the 5 percent level in comparison to two of the other individual high vigor crosses.

Considering these results in terms of the original objectives, one must conclude that, to some extent, vigor is a heritable trait of slash pine. Vigor, of course, might be estimated in a number of ways. In juvenile plants height growth should be one valie measure of this characteristic. The actual degree of genetic superiority of the selected parents is perhaps more open to question. In Table 1, mean heights of individual progenies and of various progeny groupings were given. Considering all of the seedlings for which tree 8-53 was one of the parents, the average height of this group was 9.1 feet. The average height of all check seedlings combined was 7.3 feet. This superiority of the progeny of tree 8-53 could be considered an indication of the genetic superiority of this parent. The mean height of the progeny of the other parents are also indicated and their relative ranking might tentatively be suggested as a method of evaluating the relative worth of each parent

Figure 1
Mean and Variation in Progeny Height Growth



tree. On this basis height of the progeny of the low vigor cross, while lower than that of the high vigor crosses, does not indicate any genetic inferiority to the population mean suggesting that it might be more difficult to select for low rather than high vigor in mature trees.

The third objective of the study was to determine the validity of genetic evaluations made on the basis of phenotypes. It would appear that the pehnotypic comparisons which were the basis of the selections did furnish an estimate of the genetic value of the high vigor trees, while the low vigor selections were less successful. Using the phenotypic comparisons of height growth in the progeny and volume of the parents we made an estimate of heritability of high vigor. Lush[1] has suggested that the ratio of progeny superiority to parent superiority constitutes an estimate of heritability. The four high vigor selected trees had an average of 135% volume superiority over the stands from which they were selected. The progeny of these trees had an average height superiority of 20% over the check sources. If volume superiority in the parental generation and height superiority in the progeny can be accepted as indications of relative vigor in the two populations, our heritability estimate is:

$$H=\frac{20.3}{135.5} = .15.$$

In other words, 15% of the extra vigor of the selected trees was passed on to their offspring. This is admittedly a tenuous heritability estimate but it does give some indication of the possibility of improvement of growth rate and vigor of slash pine through selection. This should be particularly encouraging to those who have given considerable weight to volume superiority in their selection schemes. As a word of caution, it should be pointed out that the 20% height superiority of these five year old progeny cannot be interpreted as indicating a proportional volume superiority at harvest. It is impossible to say at this time whether the differential will increase or decrease.

Another point of interest in these data is the highly significant difference between the mean heights of some of the crosses of high vigor trees. Of particular note, crosses H and J both have tree 5-52 as a female parent but different pollen parents. J has the poorest average height of the high vigor crosses while H has the greatest. It seems that trees 5-52 and 8-53 complement each other. To borrow a term from the corn breeders, tree 5-52 has good specific combining ability with tree 8-53 but much poorer specific combining ability with tree 3-53. Other similar contrasts are apparent in Table 1. One might capitalize upon good specific combining ability by establishing a seed orchard having only

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[1] Lush, J. L. 1945. Animal Breeding Plans. Iowa State College Press, Ames, 3rd Ed. 443 pp.

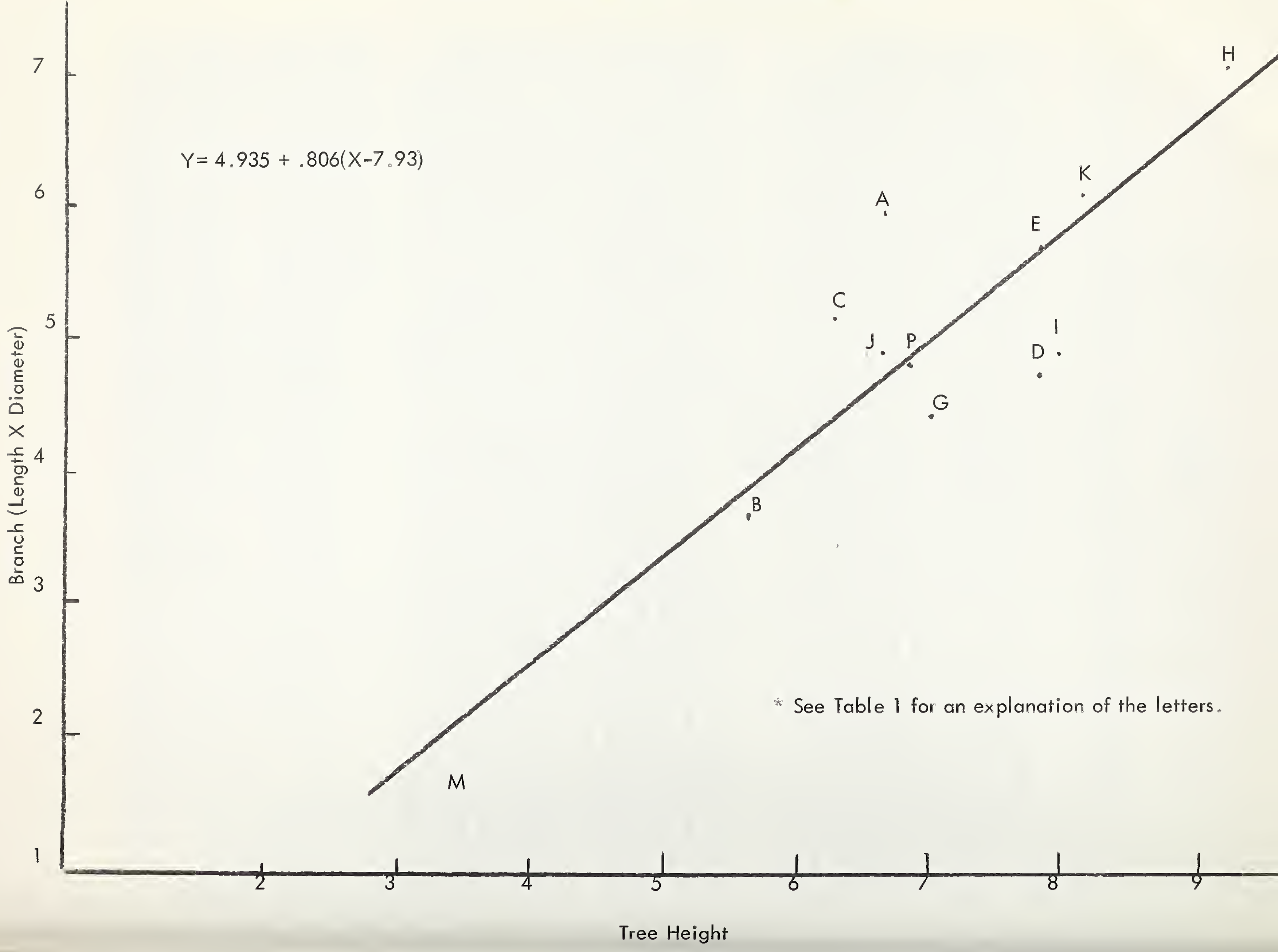
Table 1

Mean Heights of Progeny Groupings

Source	Description	Average Height (feet)
A	Austin Cary Forest check	7.68
B	Waldo Road check	6.64
C.	State Nursery check	7.43
	Combined check mean	7.29
D	2-53 x wind	8.82
E	5-52 x wind	8.84
	Open pollinated select mean	8.83
G	2-53 x 8-53	8.00
H	5-52 x 8-53	10.23
I	2-53 x 3-53	8.95
J	5-52 x 3-53	7.63
K	8-53 x 3-53	9.16
	Control-pollinated select mean	8.77
	8-53 as one parent	9.10
	5-52 as one parent	8.85
	2-53 as one parent	8.59
	3-53 as one parent	8.59
P	1-53 x 6-53 (low vigor cross)	7.70
M	2-53 x 2-53 (self-pollination)	4.54
	General mean	7.96

Figure 2

Correlation of Progeny Branch Size with Tree Height*



* See Table 1 for an explanation of the letters.

two clones which so complement each other. However the risks and disadvantages of such an arrangement probably far outweigh the possible benefits. Of greater general utility would be clones which combined well with a number of other pollen parents, that is, clones which have good general combining ability. While there is variation in performance of the individual crosses, tree 8-53 performs rather well in all the crosses in which it is involved. The two open pollinated progenies also have heights above the general check sources. These results might indicate satisfactory general combining ability. It can also be expected that there will be examples of good specific combining ability in a multi-clone orchard and that the progeny of such crosses will upgrade average performance of the general seed orchard progeny.

Thus far, the discussion has been concerned exclusively with tree height. Crown form is another indication of vigor and has, of course, important bearing on general tree quality. In this respect, there was also considerable variation among the various progeny groups. As should be expected in trees of this age, there was a close relationship between tree height and crown size. This relationship is shown quite clearly in Figure 2. In this figure, crown size is indicated by the product of the length and diameter of the limbs of the lower major whorls. This product merely gives an indication of relative branch size. Tree height and branch size has very highly significant correlation coefficient of .87. A noteworthy point in this figure is the location of G, I, and D in relation to the regression line. All of these are offspring of tree 2-53. All of the progeny of this tree tend to produce small branches in relation to their total height when compared to all other progeny in the planting. In contrast, seedlings from one of the check sources had rather large branches in relation to total tree height.

SUMMARY

Both open and controlled pollinated progeny of trees selected for high and low vigor and progeny from three check sources were established in a replicated design. Total tree height and limb size were measured five growing seasons after plantation establishment. Check sources did not differ significantly among themselves but were significantly poorer than both open and controlled pollinated high vigor selected trees in height growth. Self pollinated progeny were significantly poorer in height growth than any cross pollination. Heritability of vigor in the study was very roughly estimated as 15%. Among the controlled pollinated progenies there were definite indications of variations in specific combining ability. There was a close positive correlation between tree height and limb size.

INHERITANCE OF GUM YIELD AND OTHER CHARACTERISTICS OF SLASH PINE

By

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The extensive amount of forest genetics and tree improvement work in the South requires that we learn something of the heritability of traits with which we are working. Admittedly, heritability estimates are beset with certain assumptions and the application of specific estimates is necessarily severely restricted. In spite of this, we need them to provide some sort of estimate of expected gains from our efforts and to help guide future programs.

Highly accurage estimates of heritability require extensive data and usually it is preferable to design experiments specifically for studying it. Unfortunately, few experiments in forest genetics have been set up specifically for this purpose. Where they have been, it will be some time before reliable data encompassing an appreciable portion of rotation age will become available. Meanwhile, we will have to make use of studies originally established for other purposes.

This report presents preliminary estimates of heritability for several economically important traits of slash pine. They are considered preliminary because the progeny trees are not yet mature, relatively few parent trees are involved, and finally, because the experiments involved were not designed specifically for estimating heritability. However, the study includes observations from what is believed to be the oldest progeny test in the country that involves an appreciable number of individual tree crosses, and we believe the results will be useful.

PROCEDURE

The heritability estimates presented here are based upon three plantations described below.

1. Progeny plantation 0-116.--This plantation was established from 1-year-old seedlings in June 1946. The parents of the trees had been selected for either

high, average, or low gum yielding ability. Both wind- and cross-pollinated progenies were included. The plot layout consisted of seven blocks, each containing from 2 to 6 individuals per progeny randomly positioned in each block. Spacing was 20 x 20 feet.

2. Progeny plantation 0-146.--This plantation was established from 1-year-old seedlings in January-February 1951. The parents had been selected for high or average gum yielding ability and both wind- and control-pollinated progenies were represented. The plot layout consisted of four randomized blocks. In these blocks the cross-pollinated progenies were represented by row plots of from 15 to 18 trees each and the wind-pollinated progenies were represented by row plots of 2 to 7 each. Spacing was 12 x 18 feet.

3. Clonal plantation 0-132.--This plantation was established from rooted cuttings which were planted at various times between 1945 and 1947. The cuttings had been taken from trees selected for high, average, or low gum yielding ability. The plantation contains from 2 to 8 trees from each clone, not arranged in any type of design. Spacing was 20 x 20 feet.

Gum yields were measured by a microchipping technique in progeny plantation 0-116 in the summer of 1956. Under this technique the flow of gum is measured from 1-inch-square punch wounds over a relatively small part of a season (Ostrom and True, 1946). It seems to be fairly satisfactory as a measure of relative yield capacity. Yields in clonal plantation 0-132 were measured in the summer of 1960. Progeny plantation 0-146 has not yet been tapped for gum, because the trees are a little undersize for that purpose.

Diameters, total heights, branch lengths, and bark thickness were measured in the late fall of 1959 or winter of 1959-1960. Average branch length was measured at a point 12 feet from the top of the tree. Bark thickness was measured at Breast height at 4 points uniformly spaced around the stem of the tree and averaged.

The statistical procedures used in estimating heritability were patterned largely after those employed by Robinson et al. (1949) and Falconer (1960). Time will not permit a full discussion of the statistics involved. One procedure is to run an analysis of variance on the progeny or clonal data and then estimate the genetic and environmental components of variance. Heritability is then computed as the proportion of genetic to total variance, expressed in percent. In another procedure the parent-progeny regression or correlation provides an estimate of heritability. In still another method called the "selection experiment method" the amount by which the selected parents exceed the population average. More details of the methods employed will be covered in another report.

In analyzing cross-pollination data, the matings were pared off into groups of two, each group containing a common female. In such a case the female component is the best estimate of additive genetic variance (or "breeding value") but where the male component is not appreciably larger both can be used (Falconer, 1960). Of course, larger groups having a common female (or common male parent) are preferable if available.

The wind-pollinations similarly provide an estimate of additive genetic variance. Ordinarily one assumes that the wind-borne pollen is genetically uniform and equally effective for all seed parents. Under this assumption one multiplies the additive genetic variance by 4 to estimate heritability (because the component of genetic variance estimated is 1/4 of the theoretical value under the assumption). However, the parents may be growing in different areas in which case the wind-borne pollen may be genetically different because of racial effects. A similar situation may be true even for trees within the same stand; that is, pollen in the immediate neighborhood of one selection may be genetically superior to that surrounding another selection. Finally, the selections may have different degrees of selfing or other types of inbreeding. All these factors tend to exaggerate the estimate of additive genetic differences. If one assumes that the wind-borne pollens effective on each tree are completely different, the computed additive genetic variance should be multiplied by 2 instead of 4 (because the genetic component estimated is 1/2 of the theoretical value under this assumption). In order to take into account these sources of error the estimates of heritability for wind-pollinations presented herein are given as a range between two values representing the two extreme cases discussed (that is, multiplying genetic variance by 2 and 4 respectively).

The estimates of heritability computed for clonal data include non-additive genetic effects (dominance and epistatic deviations) in addition to additive ones. Under most situations only the additive variance is considered pertinent. Therefore, estimates obtained from clonal data, which will usually be higher than those from progeny data, should be considered maximum estimates of heritability.

RESULTS

The progeny and clone means for each trait studied are presented in tables 1 and 2, to give an idea of the extent of presumably genetic variation in each trait. Note that the variation is much higher for gum yield than for other traits. This is largely because the parents were selected for high-gum-yielding ability only. In respect to the other traits, the trees can be considered random, although the possibility of linkage with gum yield exists. In any event, even the variation among these is fairly substantial. For example, the wind-pollinated progenies of plantation 0-116 varied from an average 7.9 inches d.b.h. to 9.1 inches, a spread of about 15 percent. A purposive selection for d.b.h. would likely have resulted in still greater variation.

The estimates of heritability obtained from analyses of variance among progeny data are presented in table 3. Estimates obtained by other procedures will be discussed under the appropriate traits.

Table 1.--Progeny means of various traits for which estimates of heritability were made.

Progeny	Basis, trees	Gum yield[1]	d.b.h.	Stem volume	Total height	Branch length[2]	Bark thickness[3] Actual	Bark thickness[3] Adjusted[4]
	Number	Grams	Inches	Cu.ft.	Feet	Feet	Inch	Inch
PLANTATION 0-116--CROSS-POLLINATIONS								
G1* x G2*	27	260	8.7	7.9	40	7.9	.72	.72
G1* x G7*	27	195	9.3	9.1	40	8.8	.78	.76
G3* x G2*	27	195	9.0	8.2	40	8.4	.83	.82
G3* x G6	12	123	9.4	9.4	40	8.8	.88	.85
G6 x G3*	13	108	8.4	6.5	36	8.3	.81	.83
G6 x G8	27	109	8.6	7.7	40	8.2	.82	.83
PLANTATION 0-116 -- WIND-POLLINATIONS								
G1* x wind	38	166	8.8	8.0	39	8.6	.81	.80
G2* x wind	37	194	8.8	8.4	42	7.5	.75	.74
G3* x wind	36	154	8.9	8.0	39	8.4	.84	.83
G4* x wind	18	191	8.6	7.6	40	7.3	.80	.80
G6 x wind	34	91	7.9	6.0	38	8.0	.76	.79
G8 x wind	17	149	8.6	7.7	41	8.6	.84	.84
G23 x wind	33	123	8.1	6.6	40	8.3	.69	.73
G25 x wind	39	217	9.1	8.3	39	8.2	.86	.83
PLANTATION 0-146--CROSS-POLLINATIONS								
G1* x G5*	64	--	3.8	--	20	--	--	--
G1* x G9*	68	--	3.8	--	20	--	--	--
G10* x G5*	70	--	3.4	--	18	--	--	--
G10* x G11*	64	--	4.0	--	20	--	--	--
PLANTATION 0-146--WIND POLLINATIONS								
G3* x wind	25	--	3.7	--	19	--	--	--
G8 x wind	26	--	3.7	--	20	--	--	--
G10* x wind	26	--	3.8	--	20	--	--	--
G13 x wind	27	--	3.8	--	19	--	--	--
G31 x wind	22	--	3.8	--	20	--	--	--
G36 x wind	16	--	4.4	--	22	--	--	--
G37 x wind	24	--	3.9	--	20	--	--	--

*Phenotypically selected for high gum yield; all other parents were average or low gum yielders. [1] Yields were obtained from microchipping in the summer of 1945 (4 biweekly streaks, 1-inch square, acid-treated). [2] Branch length was measured at a point 12 feet from top of tree. [3] Bark thickness was measured at 4 points uniformly spaced around stem of the tree at d.b.h. and averaged. [4] Adjusted for apparent effects of d.b.h. by covariance techniques, to a common d.b.h. of 8.9 (b=.058) for controlled pollinations and to a mean of 8.6 for wind pollinations (b-.047).

Table 2.--Clonal means for d.b.h., gum yield and bark thickness. (Rooted cutting plantation, 0-132)

Clone number	Basis, trees	D.B.H.	Gum Yield Actual[1]	Gum Yield Adjusted[2]	Bark thickness Actual[3]	Bark thickness Adjusted[4]
	Number	Inches	Grams	Grams	Inch	Inch
G-1*	6	6.1	820	807	0.60	0.56
G-2*	8	5.4	685	693	.54	.54
G-3*	2	5.2	528	534	.52	.53
G-4*	6	3.8	596	632	.41	.50
G-5*	3	3.8	579	620	.40	.48
G-10*	4	2.8	---	---	.34	.48
G-11*	4	7.9	1,348	1,293	.81	.67
G-12	2	7.8	266	208	.70	.56
G-28*	3	5.3	---	---	.53	.54
G-31	2	4.8	211	226	.48	.50
G-35	3	6.4	471	448	.49	.43
G-36	2	4.1	127	158	.45	.52
G-37	3	5.9	348	337	.55	.52

*Phenotypically selected for high gum yield; all other parents were average or low gum yielders.

1. Yields were obtained from microchipping in the summer of 1960 (12 biweekly streaks, 1-inch square, acid treated).

2. Adjusted for apparent effects of d.b.h. to a common d.b.h. of 6.0 inches (b=22.85).

3. Bark thickness was measured at 4 points uniformly spaced around stem of tree at d.b.h. and averaged.

4. Adjusted for apparent effects of d.b.h. to a common d.b.h. of 5.3 inches (b-.055).

Gum Yield

The estimates of heritability given by Squillace and Dorman (1959), plus an estimate made from recent data on the clonal plantation, indicate that the heritability of gum yield under the conditions tested is quite strong. The various estimates obtained are tabulated below:

Method	Heritability (Percent)
Selection experiment	45
Regression of offspring on mid-parent yields (cross-pollinations)	56
Regression of offspring on female parent (wind-pollinations)	62
Components of variance among wind-pollinated progenies	45 to 90
Components of variance among clones	90

The actual estimate given by Squillace and Dorman for components of variance among wind-pollinated progenies was 90 percent. However, for reasons discussed earlier, all estimates based on components of variance in wind-pollinations are shown as a range of values as indicated.

The first three estimates listed are based upon both parental and progeny data and the heritabilities apply to selection under conditions existing for the parents. The latter two are based upon progeny and clonal data only, and the estimates apply to selection under conditions existing in the plantations. This probably partially explains the relatively lower estimates (45 to 62 percent) in the former and the higher ones (45 to 90 percent) in the latter. This important point will be elaborated upon later.

In all of the foregoing estimates for heritability of gum yield, except possibly the "selection experiment" estimate, we must recognize that the parents were not randomly selected. Non-randomness, on the average, tends to exaggerate heritability. In computing the estimate only by components of variance for the wind-pollinated progenies we were able to take this difficulty into account. The parent trees were grouped into high and

Table 3.-- Estimates of heritability of various traits obtained for progeny data from Plantations 0-116 and 0-146 by components of variance methods.

Trait	Plantation 0-116		Plantation 0-146	
	Cross-pollinations	Wind-pollinations	Cross-pollinations	Wind-pollinations
	Percent			
Gum yield	--	45 to 90	--	--
D.B.H.	33	29 to 58	21	5 to 10
Stem volume	31	18 to 35	--	--
Total height	13	8 to 16	11	5 to 10
Crown width	12	24 to 48	--	--
Bark thickness	57	33 to 67	--	--

average gum yielders and the variances were computed within these groups separately. The estimate, therefore, is probably conservative and we still came up with 45 to 90 percent. Thus, we feel that the remaining values are fairly reliable The cross-pollinated progenies could not be grouped in a similar manner, and hence no estimate was made for them.

Prior to obtaining the estimate for the clonal plantation we found that gum yield from microchipping was significantly correlated with d.b.h. within clones. Therefore, actual yields were first adjusted for effects of d.b.h. Also, as indicated earlier, the estimate from clonal data includes non-additive genetic variance. This, coupled with non-randomness of the clonal plantation, reduces the reliability of the estimate based on these gum - yield data.

D.b.h.

The estimates of heritability of d.b.h. were variable, ranging from 25 to 58 percent for the wind-pollinated progenies of plantation 0-116 to 5 to 10 percent for the wind-pollinated progenies of plantation 0-146. The variation is not surprising because, as pointed out earlier, the separate analyses are based upon relatively few parents.

Stem Volume

The two estimates of heritability for stem volume were 31 percent and 18 to 35 percent, which are not highly erratic and probably reasonable.

Total Height

The four estimates for total height were surprisingly consistent and low, varying from 5 to 16 percent. They are considerably lower than the estimates for d.b.h. or stem volume. We can only speculate as to the cause of this. A significant point may be that the spacing was quite large in both plantations and crown competition has not yet been very severe. Thus, it is possible that under such conditions genetic variability in height growth has not had an opportunity to become expressed Under a normal, closer spacing results may have been different

Crown Width

The two estimates of heritability for crown width were low (12 percent) to moderately high (24 to 48 percent).

Bark Thickness

The two estimates of heritability obtained for bark thickness from the progeny data were rather high and fairly consistent (57 and 33 to 67 percent). Bark thickness was found to be rather strongly related to d.b.h. and a covariance technique had to be used. Thus, the estimates of heritability of bark thickness are independent of d.b.h. In the same manner an estimate of 52 percent was obtained from the clonal data.

DISCUSSION

Heritability estimates provide a measure of the gains expected from phenotypic selection. However, a specific estimate applies to the conditions under which the experiment was conducted. This is because heritability depends on environmental as well as genetic effects. If two groups of trees are of identical genetic constitution, one could get different estimates of heritability if they are growing on different sites or if they are evaluated with different accuracies.

Thus, for example, parental selections in this study are growing in diverse stands on different sites and they were of different ages. Their gum yielding ability was evaluated in comparison with surrounding trees, taking into account the effects of diameter. Now in applying heritability determined from such data one assumes that selection will be made under the same conditions. On the other hand, the progenies were growing in a nicely replicated plantation, with a large portion of the site effects accounted for by randomized blocks. When heritability is computed on the basis of progeny data alone the estimate will likely be higher, but such estimates then apply to plantation conditions, with selection to be made within small areas of uniform site in the plantation.

On the basis of gum yield results one might conclude tentatively that the heritability of gum yield among trees growing under natural conditions and evaluated in the manner described is about 55 percent. Thus, if one selects trees under these conditions and establishes orchards he can expect to gain about 55 percent of the selection differential (the difference between average yielding ability of selections and the average for the whole population).

Heritability of gum yield under plantation conditions is likely somewhat higher, possibly about 70 percent. Thus, if selections are made within small uniform areas in plantations one can expect to gain about 70 percent of the selection differential.

On the basis of the results presented for other traits, we can probably say that the heritability of d.b.h., stem volume, and branch length under plantation stand conditions was weak to moderately strong, in the neighborhood of about 25 percent. The heritability of total height was consistently weak, about 10 percent. For bark thickness it was rather strong, about 50 percent. Heritability of these traits under natural stand conditions would very likely be less.

As cautioned earlier, these results are not based upon ideal data for estimating heritability and the samples were small. Nevertheless they are our best estimates and probably have some merit.

Taking them at their face value it would appear that phenotypic selection for high gum yield, even in natural stands, would pay high dividends. In other words, if trees are selected in the manner done in this study, substantial gains could be made merely by phenotypic selection and establishment of clonal orchards or seedling orchards from crosses made among them, without progeny testing. Likewise, even seed-production areas with trees selected on basis of gum yield tests would likely pay off. Of course, progeny testing would provide even higher gains. The same would probably be said for bark thickness if it were advisable to select for such a trait. The high estimates for these traits also suggest that relatively few trees need be progeny tested to obtain a sufficient number of superior trees for orchards. Testing of about twice the number required for orchards would be adequate, although other considerations may affect one's decision here.

Heritability among the remaining traits, as they apply to selection in plantations, was weak to moderately strong. As indicated earlier, it would likely be even less under natural stand conditions. Therefore, it would appear that when selecting under natural stand conditions, progeny testing is necessary to ensure that we make appreciable gains. Under plantation conditions phenotypic selection within small areas of uniform site without progeny testing may be worthwhile. The relatively low heritabilities for these traits also suggest that relatively large numbers of trees should be progeny tested.

Irrespective of the type and intensity of selection required, the genetic variation found for all traits considered in this study suggests that we are getting somewhere with out tree improvement efforts.

LITERATURE CITED

Falconer, D. S.
1960. Introduction to quantitative genetics. Ronald Press Co., New York. 365 pp.

Ostrom, C. E., and True, R. P.
1946. A "test-tube" method for experiments in gum flow. AT-FA Jour. 9(2):10.

Robinson, H. F., Comstock, R. E., and Harvey, P. H.
1949. Estimates of heritability and the degree of dominance in corn. Agron. Journ. 41:353-359.

Squillace, A. E., and Dorman, Keith W.
1959. Selective breeding of slash pine for high oleoresin yield and other characters. (Abs.) 9th Internatl. Bot. Cong. Proc. 1959: 375.

GROWTH, CROWN FORM, AND FUSIFORM RUST RESISTANCE IN OPEN-POLLINATED SLASH PINE PROGENIES[1]

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The Ida Cason Callaway Foundation began an active program in tree improvement in 1950. Their program was devoted to selection and progeny testing among the four major species of southern pines. Field plantings were made first in 1952 with open-pollinated progenies from individual selected trees and establishment continued until 1957. During this period a large number of tests were established of both open-pollinated and control-pollinated progenies. The properties of the Foundation lie north of the natural range of slash pine, but several plantations 15 years of age or younger were available and selections from these plantations were the parents used in the slash pine tests.

The area of plantations available and their ages placed restrictions on the selection of "plus" trees. A number of good phenotypes were chosen for testing, but many of the trees had only one or two good traits. Some trees, such as C-4 and C-6, were included because of undesirable traits, such as crook and poor branching. The limited population sampled means that only a few of the Callaway selections of slash pine would be comparable to the plus trees being used in current seed orchard programs.

Periodic measurements have been made on the Callaway material through 1959. This paper deals with results of measurements taken on the 1952 plantings through 8 years in the field and the 1953 plantings through 7 years in the field. The progenies were planted in replicated randomized block designs on a Piedmont old-field site that was quite variable because of erosion and top soil removal in the past.

The 1952 study showed a range in average heights among 19 progeny groups from 19.4 to 25.0 feet at 8 years of age (Table 1). This study had three replications with plots of varying sizes. Through the fourth year, significant differences were found between mean heights among progenies. At ages 6 and 8, differences among mean progeny heights were found to be not significant, in spite of the large differences among means.

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[1] Prepared for presentation at the Sixth Southern Forest Tree Improvement Conference Gainesville, Florida. June 7 and 8, 1961. These data are based on a portion of a thesis submitted for the Ph. D. degree at the University of Minnesota.

The 1953 planting showed a range in mean heights from 16.0 to 21.6 feet at 7 years (Table 2). Significant differences in height were found at all ages examined, though the level of significance dropped from 1 percent to 5 percent at ages 5 and 7. This study had 4 replications of 25 tree plots.

When examined on an individual tree basis, total height after 2 years in the field correlated well with total height at ages 8 and 7. The correlation coefficients varied from 0.61 to 0.72, depending upon whether or not trees containing stem cankers of fusiform rust were included. Using an approximate method of analysis based on within-plot variation, the Block X Lot interaction was found to be highly significant in both studies. This interaction was also examined in several of the younger studies and was found to be highly significant in every instance but one. This means that the various progeny groups are more sensitive to site variation than had been anticipated. In terms of progeny test design, it means that we must find more uniform sites and then sample several of these uniform sites in order to get our most sensitive trees.

Average eight-year d.b.h. values ranged from 4.4 to 5.4 inches in the 1952 study and 7-year d.b.h. values from 3.2 to 4.9 inches in the 1953 study. Analyses indicated that there were no significant differences among progenies in the older study, but highly significant differences in the 7-year material. This again is probably attributable to study design and the variability in site. When examined on an individual tree basis, d.b.h. was found to be highly correlated with total height, with correlation coefficients varying from 0.83 to 0.88.

The relationship of d.b.h. to number of trees surviving per plot was examined in the 7-year-old material. The regression was found to be positive and highly significant. The positive regression is contrary to normal expectations. It is generally accepted that the fewer trees per unit area, the larger the diameter of the individual tree. These data were to the contrary. The explanation probably lies in the relationship of the inherent vigor of the progenies to survival, and possibly in the relationship of survival to site variation. It appeared that the progenies that survived best grew fastest and though the number of trees competing on each plot was greater, the trees grew at a faster rate so that they had larger diameters. The relationship of total height to survival was also examined and a similar positive significant regression was obtained. It is impossible from these data to determine which portion of this relationship is attributable to inherent vigor and which portion to site variation. If this relationship is attributable in a major part to inherent vigor, it will seriously complicate adjustments that should be made in analyses to account for mortality and resulting differential competition, because mortality will be confounded with inherent vigor.

Table 1.--Mean values for various characteristics of open-pollinated progenies of slash pine, study 102 (1952)

Lot	Average height[1]	Average d.b.h.[1]	Rust free[2]	Crook[2]	Crown width[3]
	Feet	Inches	Percent	Percent	Ratio
C-4[4]	22.40	5.02	59	90	0.54
C-6	21.44	4.99	47	74	--
C-7	21.50	4.54	41	70	--
C-10	22.20	4.82	52	51	.54
C-37	22.73	4.84	70	63	.44
C-50	22.55	4.60	41	68	.38
C-51	22.12	4.76	50	62	--
C-54	24.34	5.15	88	63	.42
C-56	24.99	5.16	49	61	.44
C-59	20.89	4.23	73	74	--
C-60	22.10	4.83	48	90	--
C-61	21.65	4.81	60	39	--
C-62	22.03	4.74	37	40	--
C-63	23.96	5.35	76	66	.40
C-65	23.92	4.95	61	63	--
Sou. Miss.[5]	19.79	4.61	19	67	--
New Orleans[5]	19.43	4.44	26	72	--
Control Seedlings[6]	21.23	4.75	37	54	.52
Control Seed[7]	23.07	4.87	35	70	.53

1. Data recorded after 8 years in the field.
2. Data recorded after 6 years in the field.
3. Data recorded after 3 years in the field.
4. The "C" designation before a number indicates a selection of the Callaway Foundation.
5. Mixed lots obtained from Southern Forest Experiment Station, Forest Service, U. S. D. A.
6. Seedlings obtained through normal public distribution channels, source unknown.
7. Seed purchased from a commercial seed dealer, 1950.

Table 2.--Mean values for various characteristics of open-pollinated progenies of slash pine, study 103 (1953)

Lot	Average height[1]	Average d.b.h.[1]	Rust free[2]	Crook[2]	Crown width[2]
	Feet	Inches	Percent	Percent	Ratio
C-4[3]	18.46	4.12	69	79	0.49
C-6	16.82	3.92	66	74	.48
C-7	19.86	4.30	51	59	.41
C-10	19.88	4.40	58	50	.47
C-37	21.60	4.92	73	60	.39
C-50	20.82	4.30	48	72	.40
C-51	17.42	3.96	78	38	.41
C-58	20.95	4.31	56	77	.42
C-63	20.10	4.26	60	66	.41
C-65	18.99	4.04	71	54	.42
C-134	18.16	3.81	53	73	.41
Sou. Miss.[4]	16.57	3.44	38	66	.45
New Orleans[4]	17.76	3.79	48	70	.45
CA-82[5]	18.84	3.95	32	68	.42
CB-23[5]	17.53	3.53	32	55	.48
CB-74[5]	16.16	3.30	38	30	.43
A-1[6]	17.60	3.56	48	86	.46
A-2[6]	17.45	3.52	57	72	.51
Control Seedlings[7]	16.00	3.24	45	54	.47
Control Seed[8]	17.66	3.84	67	60	.45
Callaway[9]	18.27	4.02	69	89	.45

1. Data recorded after 7 years in the field.
2. Data recorded after 5 years in the field.
3. The "C" designation before a number indicates a selection of the Callaway Foundation.
4. Mixed lots obtained from the Southern Forest Experiment Station, Forest Service, U.S.D.A.
5. Open-pollinated seed from selections made in Australia.
6. Open-pollinated seed from selections made near Auburn, Alabama.
7. Seedlings obtained through normal public distribution channels, source unknown.
8. Seed purchased from a commercial seed dealer, 1951.
9. Seed collected from dominant and co-dominant, rust-free trees at the Callaway Foundation for use in routine planting operations.

A measure of natural pruning was taken by recording the height to the lowest whorl having two or more live limbs. Striking differences were observed among progenies; some lots and individuals displayed distinct tendencies toward early natural pruning, though lateral branch competition was very low.

Crown widths were examined in the progenies at ages from 3 to 5 years. In the 1952 study, the ratios of maximum crown width at 1/3 the height of the tree to total tree height were determined and the values analyzed. The range of progeny means varied from 0.39 to 0.55 and highly significant differences were found among progenies. Similar ratios were determined for the 1953 planting at 4 years of age and highly significant differences amont progenies were obtained, with ratios varying from 0.34 to 0.47. At 5 years of age, the 1953 plantings were examined and the crown-width measurements were taken at 1/2 the height of the tree and similar ratios were determined. These ratios varied from 0.39 to 0.51 and differences among progenies were highly significant.

In 1959, detailed measurements were made on certain crown characteristics in selected progenies, and 267 variables were examined in a correlation analysis. Using data collected from whorls of branches that had completed 3 growing seasons, we have found several interesting points (Table 3.). Branch length was highly correlated with branch diameter (0.95). Branch length and branch diameter were both negatively correlated with branch angle (-0.43 to -0.48). Branch length was weakly correlated with amount of stem growth above the whorl; that is, total height growth during the same period that the branches grew in length (0.18 to 0.28). Branch diameter was well correlated with d.b.h. (0.53 to 0.75), and this correlation was better than the correlation of branch diameter with the stem diameter above the whorl (0.36 to 0.55). Branch length and diameter are negatively correlated with angle. Thus, as we select trees that have more nearly horizontal branches, there will be a tendency for these branches to be shorter in length and smaller in diameter.

Some of the parent trees included in these tests had varying amounts of crook in their stems. The 1952 plantings were examined at 6 years of age, the 1953 plantings at 5 years of age, and a record was made of stem crook. This was an occular estimate and may be biased. All of the biases, however, are probably in the same direction, and tend to be on the severe side. The percent of trees containing crook varied from 39 to 90 percent among progenies of the 1952 planting and 30 to 89 percent among progenies in the 1953 planting. These differences among means of progenies were significant at the 5 percent level in the 1952 planting and at the 1 percent level in the 1953 planting. The parents that had a greater amount of crook had progenies that were among those having the greatest percentage of crooked stems.

Table 3.--Correlations between various characteristics of open-pollinated slash pine progenies at ages 7 (1953 planting) and 8 years (1952 planting).

Characteristics correlated	Planted 1952[1]	Planted 1953[2]
	Coefficient	
Branch length with branch diameter	0.95	0.95
Branch length with branch angle	- .48	-.47
Branch diameter with branch angle	- .43	-.46
Branch length with stem growth above whorl	.18	.28
Branch diameter with d.b.h.	.53	.75
Branch diameter with stem diameter above whorl	.36	.55

1. n=100

2. n-59

Tallies of the number and location of fusiform rust cankers were made in the 1952 planting at 6 years of age and the 1953 planting at 5 years of age. The percent of trees free of rust was examined for both studies and in a combined analysis. The 1952 planting varied from 19 to 88 percent of the trees free of rush and highly significant differences were obtained from progenies. In the 1953 planting the percentage of trees free of fusiform rust varied from 32 to 78 percent and the differences were also highly significant. There were 11 parents or lots which were represented in both studies. The parent trees were represented by different collections of open-pollinated seed made in consecutive years. A combined analysis of variance was run to examine the relative performance of progenies of the parent trees. In the analysis, "Lots" once again showed significance at the 1 percent level and "Years" was also significant. The Lot X Year interaction was not significant. This means that the open-pollinated progenies gave similar estimates of the parent trees, though the seed were collected and planted in different years.

The relationship of fusiform rust infection to inherent rate of growth was examined by correlating the number of fusiform cankers per tree with the growth of the individual tree at early ages. For the 1952 planting, rust infection at 6 years of age in the field was very weakly correlated with total height at 2 years (0.16), total height at 3 years (0.12), second-year height growth (0.15), third-year height growth (0.03), and second-plus third-year growth (0.10). For the 1953 plantings rush infection at 5 years in the field was similarly weakly correlated with total height at 1 year (0.11), total height at 2 years (0.13), second-year growth (0.12), third-year growth (0.02), and second-plus third-year growth (0.08). All of these correlation values are very low, and from a practical viewpoint we can probably consider that the relationship of fusiform rust infection to inherent growth rate is negligible. It is apparent that even under severe field conditions some of the faster growing progenies remain free of fusiform rust cankers. Where furiform rust is as heavy as in the Callaway tests, it is unlikely that this could be attributed to "escapes".

Throughout these tests, it was found that the open-pollinated progenies in the 1952 planting and the 1953 planting were in agreement for individual parents. Though the seed were collected in different years, they tend to give the same relative estimates of the parent trees. The characteristics that seemed most variable were total height and d.b.h. These characteristics, of course, are probably more sensitive to site variation than any of the others examined. These tests have established that open-pollination can be relied on to give valid relative estimates of individual parent trees.

Analyses of data from these tests point up several matters that should be considered in progeny tests design. The interaction between progenies and blocks indicates the importance of using uniform sites and better samples of site conditions for testing trees.

Crown data of older progenies based on measurements in a single whorl appear to give reliable estimates of general crown characteristics. The examination of fusiform rust data collected from these studies show that if a severe rust year occurs at an early age, data following this will give a reliable estimate of the susceptibility of the individual trees among the progenies. It was also found that the presence of stem cankers of fusiform rust is detrimental to growth of the tree and that if estimates of the inherent ability of a progeny to grow are to be considered, one must eliminate all trees having stem cankers of rust. Otherwise, those progenies with heavier infections will be biased downward.

In addition to the material reported in this paper, other measurements were taken on the progenies and on a number of the parent trees. Characteristics, such as bark thickness, forking, and natural pruning were considered and analyzed. Information on these characteristics and more details on those reported in this paper will be published at a later date.

ARTIFICIAL TESTING OF INTRA- AND INTERSPECIES SOUTHERN PINE HYBRIDS FOR RUST RESISTANCE

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At the Southern Institute of Forest Genetics, research on disease resistance has been concentrated on *Cronartium fusiforme*, the southern fusiform rust. This rust continues to be a serious problem in southern forest tree nurseries and in plantation establishment and management.

The main purpose of the research is to determine how much variation in rush resistance occurs in southern pines and to what extent differences are heritable. The current program includes studies on intraspecific slash pine progenies from both rust-free and rust-infected parents. In addition, interspecific crosses have been made between the highly resistant shortleaf pine and the susceptible slash and loblolly pines.

In most of the testing for resistance, cotyledon-stage seedlings have been artificially inoculated by techniques similar to those previously reported (5). Initially, tests were with one-parent progenies of rust-free slash pines. Parents yielding progenies with indications of resistance have been used for intraspecific breeding among themselves and with rust-infected parents.

In 1959, 80 progenies from each of 4 types of intraspecific slash pine crosses were tested in 5 randomized blocks. The parental cross-types were: free x free, free x infected, infected x free, and infected x infected. Six weeks after inoculation, 91 to 100 percent of the progenies had leaf symptoms; there were no significant differences among the cross-types. In 7 months following inoculation, all progenies of infected parents were galled, while 91 percent of the free x free progenies had galls. None of the differences among cross-types were statistically significant.

A similar test in 1960 utilized 180 progenies from each of 3 parental cross-types: free x free, infected x free, and infected x infected. Leaf symptoms appeared on 99 percent of the progenies in 6 weeks. At 7 months after inoculation 67 percent of the free x free progenies were galled, as compared to 96 and 99 percent of the infected x free and infected x infected progenies. The free x free progenies were significantly (at the 5-percent level) less susceptible. Table 1 summarizes the results from the free x free crosses inoculated in 1960. Although the percent of progenies with foliar symptoms

Table 1.--Infections following artificial inoculation, with C. fusiforme, of intraspecific slash pine progenies from rust-free parents

Parent tree numbers		Inoculated	Six weeks after inoculation		Seven Months After Inoculation	
♀	♂		Living	Proportion with leaf symptoms	Living	Proportion with stem galls
		Number	Number	Percent	Number	Percent
18-27	18-14	39	32	97	32	53
8-7	18-14	9	8	100	8	25
17-11	9-2	36	21	100	21	52
18-27	9-2	29	27	100	27	48
11-6	18-14	42	37	100	37	97
11-6	8-7	25	18	100	18	94

was uniformly high for all crosses, the percentage of progenies ultimately galled was, in most cases, considerably smaller. The exceptions were progenies from 2 crosses having a common female slash pine parent, 11-6; in these, about the same proportion were galled as had exhibited symptoms. The data suggest that parent 11-6 transmits high susceptibility. This is further emphasized by the fact that when parents 8-7 and 18-14 were crossed with each other and parents other than 11-6, the percent of galled progeny was considerably reduced. The main point of interest from the intraspecies tests is the rather strong suggestion that crossing carefully selected rust-free parents may result in progenies with some degree of resistance.

Also tested in 1960 were progenies from 4 slash x shortleaf crosses, 1 shortleaf x slash, and 1 shortleaf x loblolly cross. Results are summarized in Table 2. Foliar symptoms, similar to those described on slash pine (5), were present 6 weeks after inoculation on 41 to 95 percent of the progenies. Galls, macroscopically typical for fusiform rust, subsequently formed on some progenies from each interspecies cross. In earlier trials (3,4) artificial inoculation of similar interspecies shortleaf hybrids resulted in foliar symptoms but no gall development; and field-planted shortleaf x loblolly hybrids have remained free of fusiform rust through 5 years of field exposure in an area of high rust incidence (1). Nevertheless, in the present study the symptom-bearing needles and the resulting galls had characteristic hyphae and haustoria of C. fusiforme (2) when examined under the microscope.

Not only did artificially inoculated interspecific shortleaf hybrids develop fusiform rust galls, but there were large differences in the proportion of galled progenies among the crosses (Table 2). In 3 crosses where shortleaf tree 2-1 was either the male or female parent the proportion of galled progenies was much higher than in the 3 cases where 2-1 was not involved. Thus different degrees of resistance, or susceptibility, appeared to be transmitted by the different shortleaf parents.

While the numbers of progenies in these interspecies tests are small, the results nevertheless establish that crossing slash or loblolly with shortleaf will not consistently yield resistant progenies. It now appears that resistance in shortleaf hybrids is more complicated than the simple dominance for resistance in shortleaf that had previously been assumed (3).

Literature Cited

1. Henry, B. W., and Bercaw, T. E. 1956. Shortleaf-loblolly hybrid pines free of fusiform rust after 5 years' exposure. Jour. Forestry 54:

2. Jewell, F. F. 1958. Stain technique for rapid diagnosis of rust in southern pines. Forest Sci. 4 42-44.

3. ___________ 1959. Disease resistance studies in tree improvement research. Proc. Fifth South. Forest Tree Impr. Conf., pp. 18-20. Raleigh, N.C.

4. __________ and Henry, B. W. 1959. Breeding for resistance to southern fusiform rust. Proc. Ninth Internat. Bot. Cong., pp. 181-182. Montreal, Canada.

5. Jewell, F. F. 1960. Inoculation of slash pine seedlings with Cronartium fusiforme Phytopath. 50:48-51.

SELECTION OF POPULUS CLONES FOR SOUTHERN BOTTOM LANDS

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In the past few years there has been an astounding increase in the demand for information about suitable methods of regenerating the various hardwood species. This interest is manifested by both foresters and landowners, but all too often there are no specific recommendations that can be made. The Stoneville Research Center of the Southern Forest Experiment Station began in 1954 to anticipate these needs. Though funds, equipment and personnel have been limited, some interesting and important results have already been obtained. After the completion of the new Southern Hardwood Laboratory, now under construction at Stoneville, progress will be more rapid.

I have been asked to tell you a little about one phase of the work, namely, the selection of Populus clones for planting southern bottom lands. It seems advisable to begin with a few words about hardwood regeneration and the general goals we hope to attain.

To repay the costs and risks of plantation establishment, which are and probably will remain higher for hardwood than for pine, superior stock, regardless of species, should possess these attributes: (1) be well adapted to survive and grow under the climatic conditions to which it will be exposed, (2) make faster-than-average growth both in height and diameter, (3) have good stem form, (4) prune itself easily, and (5) resist insects and diseases. For certain species other important characteristics might be added--for example, superior ability of a clone to root if the species is usually propagated by cuttings.

To develop such stock as rapidly as possible became our purpose. We would have liked to include in our tree-improvement all 50 of the major commercial hardwoods in the Midsouth. That being impossible, we chose the genus *Populus* as a starting point. The chief considerations were that cottonwood, *P. deltoides* Bartr., is the fastest-growing tree in North America, and growth results are therefore quickly available; that its wood has always been in good demand; that considerable work in hybridization of the genus has been reported both from the U. S. and Europe; and that we had a plentiful supply of samples of both native material and Euramerican hybrids. Euramerican hybrids, which are crosses between European species or hybrids and P. deltoides, probably are better adapted to our climatic conditions than other exotic species would be. They were recommended for our study by the late Dutch authority Dr. Houtzagers.

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Selecting the method of obtaining superior stock most suitable to our conditions was the next problem. Authorities such as Schreiner (10), Snow and Duffield (11), Wiesehuegel (13), and Rudolf (9) have pointed out that selection of "superior" trees in existing stands is a good way to begin. The next step is controlled breeding using these selected trees as parents to work toward the gathering of the good characteristics of each into a single clone where possible. Better-than-average individuals--that is, superior trees--exist in all stands, and their identification is usually not too difficult. Using them as a source of improved planting stock is a more rapid means of improving planting material than producing hybrids of proven capabilities by a program of controlled breeding, although this latter method is important as a supplemental measure.

Initially, five clones from local superior mature cottonwoods, three clones from the best 1-year-old trees in our cutting nursery, and 12 Euramerican hybrid multi-source cultivars were established and increased. Later we added several cottonwood clones and a few hybrid cultivars from Italy. A cultivar is "an assemblage of cultivated individuals which are distinguished by any morphological or physiological character(s) sufficient for man's use and maintainable as distinct under sexual or asexual reproduction"(12). A cultivar, therefore, may be derived from more than one parent tree. A clone is a cultivar derived from a single individual by asexual reproduction.

The Populus collection at Stoneville is listed in table 1, along with important attributes. Vegetative propagation by cuttings has been used exclusively to increase the planting stock available. The cultural practices were those now in general use and described in our current publication on cottonwood plantations(5). By 1959 there was sufficient stock of many of the clones and cultivars to permit the establishment of a replicated progeny test on one of the best cottonwood sites, a tract of silt loam on the bank of Lake Ferguson, near Greenville, Mississippi. These trees will be grown to maturity, at about 30 years of age, to provide opportunity to follow their development throughout this entire period and to aid in detecting any elite individuals.

Some results are already evident after 2 years. The hybrid clones differ significantly in average height. P. deltoides is very significantly taller than the average of all the hybrids combined. The greatest growth for an individual cottonwood tree in 2 years has been 30 feet in height and 4.8 inches in d.b.h. One hybrid, I 214, a spontaneous cross between P. deltoides and P. nigra (European black poplar), is very significantly better than the average of all the others combined but not better than cottonwood. In diameter growth over the 2 years P. deltoides has similarly outstripped all hybrids.

Hybrids also show significant differences in second-year survivals, which range from 25 to 100 percent. Cottonwood was not significantly different from the hybrid average nor from the average for I 214 alone, which was 100 percent.

Comparing the superior cottonwood clones with the best 20 percent of run-of-the river-bank trees revealed no significant differences in second-year heights or diameters. Survival differences among clones were very significant, but must be attributed in part, if not entirely, to age of clonal parents rather than to genetic influences. Clones from 1-year-old trees survived 100 percent; those from mature trees, only 25 to 75 percent. This corroborates earlier observations that cuttings from mature trees root less easily than those from 1- to 3-year old sprouts, but masks possible genetic differences in ability to survive.

It is still too early to be certain about some of the other attributes. Differences appear to be asserting themselves, but no statistical verification has yet been possible. However, brief mention of a few observations may be of interest.

Resistance to the leaf rusts, Melampsora spp., is quite noticeable in some instances. The hybrids P. regenerata and P. serotina, as well as the cottonwood clone Rosedale 6, have been almost eliminated from consideration because of their susceptibility. Others such as I 214 and Rosedale 8 are attacked only slightly. It should be possible to select or develop a local rust-resistant clone. We have this year obtained a variety named Siouxland which is said to have such resistance. It was originated by the Experiment Station of the South Dakota State College at Brookings, South Dakota.

In efforts to locate poplar trees that are resistant to insect attack, we have made little progress. Defoliators reduce the vigor of and sometimes kill young seedlings. Trunk borers cause defects in trees of all sizes. The twig borer, by attacking the terminal shoot, markedly slows height growth of young trees. One-year-old cottonwoods that were protected from insects have averaged 3.5 feet taller than infested trees. But while we have observed no naturally resistant trees, tests have shown that dipping cuttings to half their length in an activated carbon dust containing 44 percent of the systemic insecticide phorate (of which one of the trade names is Thimet) will protect against all troublesome insects for the first year (7). The cuttings are dipped just before they are planted. Tests are under way to determine if soil treatments with the same chemical in granular form will give protection in subsequent years.

On the basis of early results we have tentatively selected the following poplars for additional work: they hybrids *P. eugeneii*, *P. robusta*, and I 214, and the cottonwoods Catfish 2 and 5, Texas Select, Alton and Rosedale 8. The five cottonwoods and the hybrid I 214 are the best planting stock we have collected thus far for use on southern bottom lands. Except for I 214, the hybrids are slower than cottonwood and therefore are not recommended. However, they have other attributes that it seems desirable to attempt to transfer by controlled breeding into a super elite clone.

Our future efforts with *Populus* will continue to be heavily concentrated on developing elite material. The ultimate goal is to develop clones that are well adapted to a wide range of sites, that will grow 15 feet in height and 2 to 3 inches in d.b.h. each year, that will root easily, and that will produce well-formed trees while resisting insects and diseases. A large order, you say? We have already made a good start, and I believe such a goal can be achieved.

Table 1. --Populus tree improvement stock collection at the Stoneville Research Center, Southern Forest Experiment Station, as of May 1, 1961

Name	Origin	Date acquired	Under formal test	Important attributes
1. P. x euramericana (Dode) Guinier cv. 'Bachelierii'	Holland	1954	X	Poor trunk form. Susceptible to leaf rust
2. P. x euramericana (Dode) Guinier cv. 'serotina erecta'	"	"	X	Same as above
3. P. x euramericana (Dode) Guinier cv. 'eugeneii'	England	"	X	Good trunk form, but susceptible to leaf rust
4. P. x euramericana (Dode) Guinier cv. 'gelrica'	Holland	"	X	Defoliates late in fall, poor trunk form, resists leaf rust
5. P. x euramericana (Dode) Guinier cv. 'marilandica'	"	"	X	Same as above
6. P. x euramericana (Dode) Guinier cv. 'mussolinii'	"	"	X	Defoliates late in fall, poor trunk form, moderately susceptible to leaf rust
7. P. x euramericana (Dode) Guinier cv. 'regenerata'	"	"	X	Defoliates early in fall, poor trunk form, very susceptible to leaf rust
8. P. x euramericana (Dode) Guinier cv. 'serotina'	"	"	X	Same as above
9. P. x euramericana (Dode) Guinier cv. 'I 214'	"	"	X	Defoliates late in fall, good trunk form, little leaf rust, good height growth
10. P. x euramericana (Dode) Guinier cv. 'eugeneii'	"	1952	X	Defoliates late in fall, good trunk form, somewhat susceptible to leaf rust
11. P. x euramericana (Dode) Guinier cv. 'robusta'	"	"	X	Defoliates late in fall, very good trunk form, slightly susceptible to leaf rust
12. P. nigra	"	1954	X	Defoliates early in fall, poor trunk form, considerable leaf rust
13. P. trichocarpa	Washington	1959		Very poor trunk form, and very susceptible to insects and disease
14. P. x euramericana (Dode) Guinier cv. 'I 154'	Italy	1960		No observations
15. P. x euramericana (Dode) Guinier cv. 'I 262'	"	"		" "
16. P. x euramericana (Dode) Guinier cv. 'I 214'	"	"		" "
17. P. x euramericana (Dode) Guinier cv. 'I 455'	"	"		" "
18. P. deltoides (Catfish 1 from mature tree)	Miss.	1954	X	Good height growth and trunk form
19. P. deltoides (Catfish 2 from mature tree)	"	"	X	Very good stem form, slightly susceptible to leaf rust
20. P. deltoides (Catfish 3 from mature tree)	"	"	X	Poor rooting ability, some susceptibility to leaf rust
21. P. deltoides (Catfish 4 from mature tree)	"	"	X	Develops multiple sprouts, and is slightly susceptible to leaf rust
22. P. deltoides (Catfish 5 from mature tree)	"	"	X	Very good stem form, fair rooting ability, good height growth, little leaf rust
23. P. deltoides (Rosedale 6 from 1-year-old tree)	"	"	X	Very susceptible to leaf rust
24. P. deltoides (Rosedale 7 from 1-year-old tree)	"	"	X	Moderately good trunk form and height growth
25. P. deltoides (Rosedale 8 from 1-year-old tree)	"	"	X	Good height growth, slight susceptibility to leaf rust
26. P. deltoides (Texas Select-cultivar)	Ft. Worth	1958	X	Good trunk form, rapid height growth. May endure dry sites
27. P. deltoides (Arkansas Select-cultivar)	Pine Bluff	"		Rapid height growth
28. P. deltoides (Alton-cultivar)	Alton, Ill.	"	X	Good trunk form, rapid height growth, stands late freezes, little leaf rust
29. P. deltoides x P. trichocarpa (McKee poplar)	Washington	1961		Rapid early growth but considerable susceptibility to leaf rust
30. P. deltoides (cv. Carbondale 1)	Illinois	"		Rapid growth
31. P. deltoides ("Siouxland" developed by S.D. State Col.)	S.D.	"		Resistant to leaf rust
32. P. deltoides (Texas Select 1 clone)	Ft. Worth	"		Combination of rapid growth, good trunk form, and leaf-rust resistance
33. P. deltoides (Arkansas Select 1 clone)	Pine Bluff	"		Same as above
34. P. deltoides (Alton 1 clone)	Alton, Ill.	"		Same as above
35. P. deltoides (Rosedale 9 from 1-year-old tree)	Miss.	"		Rapid height and diameter growth
36. P. deltoides (Archer 1 clone)	"	"		Rapid growth; ortet grew 30 feet tall and 4.8 inches d.b.h. in 2 years

BIBLIOGRAPHY

(1) Broadfoot, W. M.
1960. Field guide for evaluating cottonwood sites. U. S. Forest Serv. South. Forest Expt. Sta. Occas. Paper 178, 6 pp., illus.

(2) Cram, W. H.
1960. Performance of seventeen poplar clones in south central Saskatchewan. Forestry Chron. 36: 204-208.

(3) Food and Agriculture Organization of the United Nations.
1958. Poplars in forestry and land use. FAO Forestry and Forest Prod. Studies 12, 511 pp., illus.

(4) Joranson, Philip N.
1959. Improvement of hardwoods through genetics. TAPPI 42: 691-700, illus.

(5) Maisenhelder, L. C.
1960. Cottonwood plantations for southern bottom lands. U. S. Forest Serv. South. Forest Expt. Sta. Occas. Paper 179, 24 pp., illus.

(6) Minckler, L. S.
1939. Genetics in forestry. Jour. Forestry 37:559:564.

(7) Morris, R. C.
1960. Control of cottonwood insects with a systemic insecticide. Jour. Forestry 58:718, illus.

(8) Moulds, Frank R.
1957. Exotics can succeed in forestry as in agriculture. Jour. Forestry 55:563-566.

(9) Rudolf, Paul O.
1956. Guide for selecting superior forest trees and stands in the Lake States. U. S. Forest Serv. Lake States Forest Expt. Sta. Sta. Paper 40, 32 pp., illus.

(10) Schreiner, E. J.
1939. The possibilities of the clone in forestry. Jour. Forestry 37:61-62.

(11) Snyder, E. B.
1959. Glossary for forest tree improvement workers. U. S. Forest Serv. South. Forest Expt. Sta., 22 pp.

(12) Snow, A. G., Jr., and Duffield, J. W.
1940. Genetics in forestry, Jour. Forestry 38:404-408, illus.

(13) Wiesehuegel, E. G.
1957. Future improvement of hardwood quality and yield through genetics. Soc. Amer. Foresters Proc. 1956: 75-78, illus.

ADVANCES IN TOOLS AND TECHNIQUES OF TREE IMPROVEMENT

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The past ten years have seen a number of development in both laboratory and field technique in tree improvement. Many of these have come as a result of the impetus of industrial interest in the program, mainly through university program cooperators. Significant advances have been made in the laboratory development of microtechniques for wood property and fibre evaluation. Although field techniques have progressed steadily, it would seem that some of them have been less well publicized than those from the laboratory. This paper will, therefore, emphasize the development of field equipment for tree improvement.

The greatest physical barrier to the forest tree breeder has been the fact that extensive flowering occurs only in the upper crown of mature specimens of the species with which we have been working. The desire to use well-formed individuals amplifies the difficulties encountered.

The first climbing was done on the west coast utilizing the recognized techniques developed by and for the tree trimming trade. The climber simply tosses a pear-shaped lead weight, with a light line attached, over a limb. He ties a heavier climbing rope to the light line, draws it up and around and climbs the rope either hand over hand or using the hand-foot technique. This, of course, is very arduous; and the height one can climb is limited by the strength of his throwing arm - and his physical condition.

The Swedish tree-climbing ladder, with which you are all familiar, was introduced about 1952 and has been a most satisfactory tool for tree climbing. Where individual trees were climbed and the area was easily accessible by motor vehicle, it has been very satisfactory. However, in concentrated climbing activities, such as in seed production areas, a ladder is needed for each person climbing. In addition, erecting and lowering the ladders is relatively slow, tedious, and demanding physically.

The Swedish tree bicycle, variously known as grimpettes or Angel Shoes, now in use in England, has been tried in several places in the United States. The task of sawing off all limbs to the live crown, however, is onerous and again the physical effort required is considerable.

Some time ago the Southern Institute of Forest Genetics inserted pole steps into one of their study trees to facilitate repeated climbing. While the steps made climbing easy, installation required a great deal effort and considerable "bleeding" followed. It was necessary to spray the entire tree with BHC to prevent insect attack. According to Bayne Snyder (13), more than 100 trees have been prepared in this manner. Incidentally, fear of encouraging beetle infestations is the main reason for banning the use of standard climbing spurs in southern pine.

In 1958, Johansen and Arline (9) at the Lake City Station developed the first extension ladder unit, which consisted of a frame for carrying and supporting the ladder and a 40-foot extension ladder. The frame can be quickly installed in a one-half ton truck bed for use and removed when the job is completed.

Several different units have been constructed from this basic design. Walt Beers (1) of Buckeye Cellulose added, as refinements, bearing mounted swivels for the main ladder, expanded metal plate for the top platform and adjustable rods for angle supports. More recently, Ed Hinkle (8) of Union Bag has adapted the same frame to seed orchard work by adding a sliding platform which extends at right angles to the truck. This enables the technicians to stand in the crown for control pollination or other seed orchard work.

At the Southlands Experiment Forest where we are doing a great deal of more or less concentrated climbing, we have pivoted the ladder frame on a trailer so that 360° rotation is possible. This minimizes the necessity of maneuvering for the best climbing position, as the trailer can be stopped at the most advantageous point and the ladder frame turned into position. For ease in raising and lowering the 55-foot ladder, a 1/2-ton hand winch is used. The Texas Forest Service (2) has added a motor driven winch to handle the ladder mechanically. No guying is necessary as the ladder is supported by the tree in every case. We have more than doubled our control pollination efficiency with this unit and have used it for seed collection with very satisfactory results. The trailer unit has a distinct advantage over the truck mounted ladder in that it can be drawn by almost any power unit available. In extremely wet weather a crawler tractor can be and has been used for maximum flotation. The best performance under most operating conditions has been with a Ford tractor equipped with half tracks.

Darroll Skilling (12) of the Lake States Forest Experiment Station recently published an article in the F A O notes showing a ladder mounted on a crawler tractor. This unit has some advantages, but would have a slow rate of operation.

An attempt was made in 1958 at Southlands Experiment Forest to use a pulley system to raise the climber into the tree, but the system was abandoned in favor of the ladder trailer. This year, Strickland and Peters (15) have developed an excellent "climbing" technique using ropes and block and tackle. A leading line is put into the tree using a sling shot. Heavier ropes are drawn into the crown and the block and tackle raised. The climber is drawn into the tree with an electric capstan or by hand. Ed Hinkle (8) reports that Union Bag has used this system very successfully.

There have been few developments in isolation bags, the standard in the South being the 3-3/4 inch sausage casing in various lengths and with a double fold stapled in one end. Last year we tried a few casings that had been commercially sealed with an aluminum cap. The cap actually was a better pollen seal than the triple fold and stood up well in the weather. This year all of our isolation bags were sealed in this manner, and we were very pleased to find that we had less damage from folding. Union Bag also used the capped bags and Ed Hinkle (8) reports less than 2% damage from folding. The standard isolation bag used by the Western Institute of Forest Genetics is made of light canvas with a plastic window glued in place. In Washington, Jack Duffield (4) uses a light, tough, weather-resistant paper bag with a cellophane window Scotch-taped in place. They also use grafting tape or rubber electrical tape to attach the bags. Their female flowers are not on first order twigs and the use of electrical tape instead of the standard cotton and wire prevents water from collecting in the isolation bag. John Matthews (10) of England is using an isolation bag made of "Terylene" non-woven fibres with a plastic window - all apparently glued in place.

Pollination syringes are fairly well standarized. There are three types in general use. First, the ordinary ear syringe with the end trimmed and a needle inserted. This is light, easy to handle, clean and re-use. With careless handling, it has the distinct disadvantage of wasting pollen, and has been thought to reduce seed set by some authorities because of over-abundant pollen introduction. Second is the plastic syringe with a single curved tube for pollen agitation. For more complete agitation, a curved tube is inserted both at the bulb and needle end of the syringe. The most complicated syringe, by Tom Perry (11), utilizes an exchangeable handle and squeeze bulb. Pollen is prevented from entering the squeeze bulb by a rubber "policeman" placed over the syringe end of the tube. There may be some danger of pollen dilution if the policeman becomes stopped in an open position. Personally, I favor the simplest pollinator with a 3/4", 16 or 20 gauge needle for ease of handling and cost.

Most of our work in this country has been in fairly concentrated areas, but in England where a good bit of ground is covered by one small group, John Matthews (10) has developed a house trailer into a laboratory on wheels. Here all his pollen is extracted and stored, and the facilities are available wherever they are needed.

The necessity of making wood characteristic analyses on living trees has led to the development of laboratory micro-techniques. These in turn have encouraged the development of techniques for removing small wood samples efficiently. The most common method of taking such samples has been with the standard increment borer which has grown larger and larger. The bit starter, available commercially, was the answer to the prayer of those who could never get the bit started. Various other aids such as the wooden plate developed by Echols (6) and the ratchet handle developed by Duffield (5) have eased the laborious process somewhat. The most rapid process for taking cores was developed at Southlands Experiment Forest by Roy Stonecypher (14). He utilized a one-inch electric drill powered by a portable generator to drive the increment borer, but backed the borer bit out by hand. A reversible drill is now being used so that except for extracting the core, the entire process is done mechanically. This gives us a better core, incidentally.

H. E. Dadswell (3) from Australia required a larger core for complete wood characterization. He has adapted a modification of the method originated by Echols and Mergen (7). Four holes large enough to allow a bow saw blade to enter are drilled through the tree trunk and, using an ordinary bow saw, a rectangular plug is removed. The hole is then sealed.

Walt Beers (1) of Buckeye Corporation has recently developed a bit for sawing out a large circular core. A one-inch drill is utilized to drive the 37-mm. core bit. The resulting hole is sealed with a sterilized barrel bung. Both Dadswell and Beers claim that holes of this size do not injure the tree.

I have presented a few of the developments in field techniques. Many more could have been cited, and there is an entire area of laboratory techniques that I have not even touched. I hope, however, that those items discussed may be of some help, and that it will be an inspirction to the "gadgeteers" in our group to further the development of tools and techniques peculiar to tree improvement work.

LITERATURE CITED

1. Beers, W. Personal Comments

2. Buijtenen, J. P. Van. Personal Comments

3. Dadswell, H. E. and A. B. Waldrop. Growing Trees with Wood Properties Desirable for Paper Manufacture. Jour. Austrailian Pulp and Paper Industry Technical Association 12 (4) : 129-136, 1959.

4. Duffield, J. W. A Ratchet Wrench for Over-size Increment Borers. Forest Science 3 (1) : 21, 1957.

5. ________________. Personal Comments.

6. Echols, R. M. Variation in Tracheid Length and Wood Density in Geographic Races of Scotch Pine. School of Forestry Bul. #64, Yale University, P. 16, 1958.

7. __________ , and F. Mergen. How to Extract Large Wood Samples from Living Trees, Jour. For. 53 (2) : 136, 1955.

8. Hinkle E. H., Personal Comments.

9. Johansen, R. W. and L. Arline. An Idea in Truck Mounted Ladders. Jour. For. 56 (11) : 852-853, 1958.

10. Matthews, J. D. Personal Comments.

11. Perry, T. O. Personal Comments.

12. Skilling, D. D. Tractor Mounted Ladder for Tree Crown Studies and Seed Collection. Forrestry Equipment Notes, A.20. 60, F.A.O. , February, 1960.

13. Snyder B., Per onal Comments .

14. Stonecypher, R.W. and F. C. Cech, An Efficent Method of Taking Large Increment Cores Jour. For. 58 (8) : 644-645, 1960.

15. Strickland, R. K. and W. J. Peters. A New Use for an Old Skl. in Tree Improvement. Res. Rept. #6 , School of Forestry, University of Florida, March 1961.

POSSIBLE REFINEMENTS IN CONTROLLED POLLINATION OF SOUTHERN PINES

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At what stage of female strobilus ("flower") development is controlled pollination most effective, in terms of seed yield?

When weather or workload makes it impossible to pollinate at this optimum flower stage, what are the earliest and latest stages at which pollination can be justified?

What is the latest stage at which pollination bags may be installed or the earliest they may be removed without danger of contamination by wind-borne pollen?

Does high laboratory germination of a compatible pollen insure good seed set if the pollen is applied to highly receptive flowers? At what level of laboratory germination percent must pollen be considered too poor to be working taking up the tree?

A definite answer to any of these questions should increase either the effectiveness or the flexibility of controlled-pollination programs. It might increase both.

In 1958 and 1959 we tried to answer these questions by control-pollinating, in various ways, 11 different prolific longleaf pine trees (Pinus palustris Mill.) near Many, Louisiana. We enclosed 1,551 flowers in 707 synthetic sausage-casing bags, as described in Southern Forest Experiment Station Occasional Paper 136, 1954. We control-pollinated with a number of different lots of both longleaf and slash pine (Pinus elliottii Engelm) pollen, both fresh and stored, as needs of individual studies dictated; in some instances we utilized wind-borne longleaf pollen also. We applied treatments in units of 5 to 10 bags per tree, and always replicated on at least 2 trees, usually on 3.

We recorded results in terms of: (1) Bags from which cones matured; (2) Percentages of flowers maturing into cones; (3) Full seeds per flower originally pollinated; and (4) Full seeds per cone matured. When only longleaf pollen had been used, we determined full seeds by cutting. When slash pollen has been applied, we expressed results in terms of viable seeds as determined by nursery sowing.

The yields of full or viable seeds per flower pollinated and per cone matured proved to be the most effective criteria for evaluating the experimental treatments, and are therefore presented in the attached tables.

Adverse weather, some individual-tree incompatibilities, insect damage to flowers and cones, depredations by squirrels, and the loss of one tree to lightning left us with fewer data than we had hoped to get. Analyses of variance although they had been planned, were applicable in none of the studies. Nevertheless some points were definitely proved and others strongly indicated, and are reported and commented on here.

Flower Stages

The 5 series of controlled pollinations described here involved recognition of from 2 to 6 of the 7 flower stages defined by Cumming and Righter in U. S. Department of Agriculture Circular 792, 1948. These are: (1) (Flower) buds small; (2) (Flower) buds large; (3) (Flower) buds opening; (4) Flowers partly open; (5) Flowers (at) maximum (receptivity); (6) Flowers closed; and (7) Cones enlarging.

We necessarily adapted and applied the classification of stages in the light of our experience with the flowers and flowering habits of the southern pines, which differ in detail from those of the western pines on which the classification was originally based.

Stage or Stages at Which to Pollinate

In 1958 we bagged at early stage 1, and pollinated separate lots of bags at stages 2, 3, 4, 5, and 6. That year, at each stage on each tree, we pollinated half the bags with longleaf pollen and half with slash. In 1959 we bagged at very early state 1, and pollinated, separately, at all stages from 1 to 6 inclusive, with slash pollen only.

The results showed definitely that pollination of bagged longleaf flowers at stage 2, with either longleaf or slash pollen, can yield a few viable seeds, and that pollination at stage 3 is quite likely to produce some seeds. The yield even from stage 3, however, is likely to be less than that from stages 4 or 5. Pollination at stage 3 only or at stage 2 only may sometimes be justifiable, but we do not recomment it for quantity production of control-pollinated seed, or (except as a last resort) for important crosses.

Flowers pollinated at what we classified as stage 4 yielded erratically. Some gave little or no seed, but in general they produced considerably more than the flowers pollinated at stage 3, and in one instance each year they excelled the best yield of flowers pollinated at stage 5. As a rule, when flowers can more conveniently be pollinated at stage 4, deferment till stage 5 seems hardly justifiable, and when flowers have been pollinated at stage 4, only extraordinary circumstances would seem to justify repollinating them at stage 5.

By and large, best results were obtained by pollinating at stage 5.

In 1958, to our surprise, our pollinations yielded almost as much viable seed from flowers we had classified as stage 6 as from those we had classified as stage 5, and more than from those we had classified as stage 4. We got some viable seed from stage-6 pollinations on one tree in 1959. As stage 6 is, by definition, past receptivity, it is evident that in practice we had misclassified as stage 6 a considerable number of flowers still in late stage 5. This misclassification raises questions as to just how dependably stages 5 and 6 can be differentiated by the unaided eye, especially when the flowers are viewed through the sausage casing. Moreover, it immediately calls into question the safety of removing bags while flowers are still in what we have been accustomed to calling stage 6.

Stage at Which to Bag

On each of 3 longleaf trees in 1959 we bagged flowers at stages l, 2, 3, and 4, at the rate of 10 bags per stage per tree.

The flowers bagged at stage 1 were exposed to wind pollination until the bags were installed. None of them received any supplemental artificial pollination.

At this point we realized that the flowers might be escaping pollination because there was as yet little or no longleaf pollen in the air, rather than because they were non-receptive. Therefore, at stages 2, 3, and 4, we dusted half of the flowers with longleaf pollen before we put the bags on.

Two trees in this study set seed from flowers bagged at stage 4, one of them from both wind-pollinated and artificially pollinated flowers, and the other only from the flowers pollinated artificially before bagging. Neither tree set seed from flowers bagged at stage 3 or earlier. The third tree set no seed from flowers bagged at any stage.

These results strongly confirm the receptivity of stage-4 flowers that was shown by the stage-of-pollination studies. In the stage-of-pollination studies there was much loose pollen in the bags. Some of this presumably could have reached the flowers, through agitation of the bags, and most or all of the viable seed must have developed from pollen grains lodging on or between the flower scales while the flowers were still in stage 4.

The results further suggest that, though receptive, stage-4 flowers (at least on the trees flowering earliest in the season) may escape pollination because of the scantiness of air-borne pollen.

The results also strongly suggest that bagging at stage 2 is amply early for controlled pollinations in which a small percentage of contamination by wind-borne pollen can be tolerated. In commercial hybridization by baggin, for example, it might be far cheaper to accept 2 percent or even 5 percent of seedlings of the female parent species than to exclude stage 2 flowers from bagging.

POLLEN GERMINATION TESTS

In 1958 we tested individual lots of 2-year-old longleaf pollen with current laboratory germinations of 92, 87, 76, 74, 65, and 58 percent against fres longleaf pollen germinating 92 percent. We applied each of the 7 pollens to flowers in stages 4 and 5 on each of 3 longleaf trees.

One tree produced a few full seeds from the stored pollen germinating 65 percent and a second tree developed a few from the stored pollen germinating 87 percent. Neither yielded full seeds from any other pollen lots, even from the fresh check.

The third tree produced full seeds from 6 of the 7 lots, but not in proportion to pollen germination per cent. In general, the fresh pollen gave the best results; in particular, it far excelled all stored lots in full seeds per flower pollinated and in full seeds per cone that matured. Among the stored lots, that germinating 65 percent yielded the greatest number of full seeds per flower pollinated. The lots germinating 74 and 87 percent were next best, in that order.

In 1959 we similarly pollinated 3 longleaf trees with 1-year-old slash pollens germinating 99, 92, and 80 percent, with fresh slash pollen germinating 99 percent. On 2 of the trees, the stored pollen germinating 80 percent equalled or excelled the stored pollens germinating 92 and 99 percent, both in viable seeds per flower pollinated and in viable seeds per cone matured. On 1 of the 2, the 80-percent stored pollen out-yielded even the fresh check. Squirrels got so many of the cones from the third tree that results can not be assessed.

It appears that pollen germinations of 90 to 99 percent in the laboratory do not insure success in crossing. At the same time, pollen germinating as little as 65 percent may be well worth using in attempts to make greatly desired crosses.

Summary and Conclusions

While the studies just described were not advanced in design or technique, they have proved or strongly indicated the following:

Bagged flowers can mature into cones and produce viable seeds if pollinated at any stage from 2 to the very end of 5. Yields from pollination at stages 4 and 5 are most certain and abundant, but pollination at stage 3 or even at stage 2 may repay the effort under some circumstances.

It is very difficult to distinguish, in practice, between flowers at the end of stage 5 (and hence still receptive) and those that have passes into stage 6 and become non-receptive. When avoidance of contamination by wind-borne pollen is imperative, flowers must not be debagged until far into or past stage 6.

When avoidance of contamination is imperative, flowers must be bagged at stage 1, but when a small per centage of contamination is preferable to excessive cost, flowers may be bagged at stage 2.

The laboratory germination indicates only roughly the capacity of the pollen to effect fertilization, and pollen germinating as little as 65 percent may be well worth using in attempts to make certain greatly desired crosses.

Table 1.--Seeds per flower pollinated and per cone matured in stage-of-pollination studies.

1958 STUDY

Pollen used and flower stage at which applied	Full[1] or viable[2] seeds, by longleaf female parents			
	Per flower pollinated		Per cone matured	
	Tree 11-4	Tree 1-16	Tree 11-4	Tree 1-16
Longleaf pollen at stage:				
2	0.2	0.0	2	--
3	9.7	1.8	33	44
4	22.8	1.2	60	32
5	22.0	9.4	66	51
6	17.1	17.9	48	78
Slash pollen at stage:				
2	.8	.0	8	--
3	1.2	.0	7	--
4	.9	.0	4	--
5	2.4	16.4	9	49
6	1.2	5.4	7	41
	1959 STUDY			
	7-24	6-6	7-24	6-6
Slash pollen at stage:				
1	0.0	--	--	--
2	.0	.0	--	--
3	1.6	.0	4	--
4	6.8	1.5	10	3
5	8.1	2.2	9	3
6	1.2	.0	2	0

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1. By cutting test in studies in which only longleaf pollen was used.
2. By seedling counts in nursery in each study in which part or all of pollinations were made with slash pollen.

Table 2.-- Seeds per flower pollinated and per cone matured in 1959 stage-of-bagging study

Pollination before installation of bags.	Flowers bagged at stage:	Full[1] of viable[2] seeds, by longleaf female parents					
		Per Flower pollinated			Per Cone matured		
		Tree 7-21	Tree 7-22	Tree 7-23	Tree 7-21	Tree 7-22	Tree 7-23
By wind only	1	0.0	0.0	0.0	--	--	--
	2	.0	.0	.0	--	--	--
	3	.0	.0	.0	26	--	--
	4	7.6	.0	.0	--	--	--
Wind plus artificial	2	.0	.0	.0	--	--	--
	3	.0	.0	.0	--	--	--
	4	33.5	6.1	.0	38	9	--

1. 2. See footnotes, table 1.

Table 3.--Seeds per flower pollinated and per cone matured in studies of laboratory germination of pollen

1958 STUDY OF LONGLEAF POLLEN

Period stored	Notes on storage	Laboratory germination	Full[1] or viable[2] seeds, by longleaf female parents: Per Flower pollinated, Tree 1-23	Per Flower pollinated, Tree 1-16	Per Flower pollinated, Tree 1-11	Per cone matured, Tree 1-23	Per cone matured, Tree 1-16	Per cone matured, Tree 1-11
Years		Percent						
0	Fresh check	92	25.5	0.0	0.0	91	0	0
2	Sealed	92	1.7	.0	.0	13	--	--
2	Sealed	87	2.4	.0	.1	5	--	3
2	Sealed	76	.5	.0	.0	6	--	--
2	Unsealed	74	3.1	.0	.0	14	--	--
2	Unsealed	65	3.4	.8	.0	11	21	--
2	Sealed	58	.0	.0	.0	--	--	--

1959 STUDY OF SLASH POLLEN

Period stored	Notes on storage	Laboratory germination	Per Flower pollinated, 7-3	Per Flower pollinated, 7-16	Per cone matured, 7-3	Per cone matured, 7-16
0	Fresh check	99	5.8	0.9	20	2
1	Unsealed	99	3.3	1.1	7	1
1	Unsealed	92	2.5	2.2	6	3
1	Unsealed	80	5.8	2.8	13	3

1. 2. See footnotes, table 1.

NATURAL AND INDUCED FLOWERING IN YOUNG PINE TREES

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In forest trees we have numerous examples of distinct growth phases, and one of the more obvious one is the formation of the first sex organs. This stage, although easily recognizable *in vivo*, presents considerable difficulties when one attempts to explain it on biochemical grounds, or induce it at will. The literature abounds with reports of the failures to induce flowering at an early age in woody plants, and almost every person interested in general field of forest genetics has at one time or another attempted to induce flowering in forest tree seedlings.

Despite the many attempts, no reliable technique has evolved that induces flowering in very young seedlings, with the exception of the grafting work by Dr. Mirov (1951). There have been, however, several successful attempts to considerably advance this "ripeness-to-flower stage". These treatments relied on either mutilation of the trees, fertilization of the trees, or on a combination of these two approaches. By this method, six-year-old slash pine seedlings, *Pinus elliottii* Engelm., were brought into flowering by Hoekstra and Mergen (1957), and Wareing (1953) was able to induce male flowers on 12-year-old Scotch pine trees. It should be realized, however, that in both instances the trees had passed the juvenile stage in many other phases of their development, e.g. foliage, bark, and wood cells.

In this maturing process, the various tree characteristics appear to progress fairly independently of each other. Although a certain trend is present, the various steps do not seem to be dependent upon each other, e.g. mature conditions in one organ do not depend on the presence of mature traits in certain other ones. As an illustration I might mention the observation where reproductive structures are produced before secondary needles are initiated. It seems to me that, although these various phases are interrelated and influenced by the environment, the physiological stages or phases of readiness for flowering proceed at their own pace and are only indirectly influenced by the maturation process in the other characteristics.

My observations on natural early flowering, as well as on induced early flowering, are based on experiments conducted over a period of six years. The observations are grouped together, as a matter of convenience, into six categories, namely: Report of early flowering; Relationship between first flowering and successive flowering; Effect of geographic seed source; Effect of hybridization; Attempts to stimulate flowers by altering the physical environment; Treatment with liquid fertilizer, high temperature and humidity; and Effect of physical and chemical treatment.

Observations

Report of early flowering: In 1939, Righter (1939) reported on the minimum ages for both staminate and ovulate flowers in 57 species and varieties of pines grown at Placerville, California. The average minimum age was 4.4 years for male flowers and 5.2 years for female flowers and one of the species bore male flowers when only one year old. During the spring of 1957, I observed male flowers with viable pollen on Mugo pine seedlings that were 10 months old (Mergen and Cutting, 1957). Three plants from a total of about 330 seedlings, bore 12, 6, and 4 catkins respectively. The catkins were of normal size, and both the percentage of germination and pollen tube growth were normal when the pollen was cultured in distilled water. Of particular interest was the fact that these three seedlings produced reproductive structures prior to the initiation of secondary needles.

Relationship between first flowering and successive flowering: The Mugo pine seedlings that flowered while less than one year old were observed for four consecutive seasons, and in each year male flowers were produced. Whether the early manifestations of flowering in pine trees are of a transitory nature or whether they are an indication of sustained reproductive activity was discussed by Righter (1939). He felt that these early flowering were reliable indications that additional flowers would appear. A check on the relationship between the first flowering and flowering in the succeeding year was made on 14 different species and pine hybrids in my progeny testing plantations. A total of 89 trees were involved in the test. A regression analysis, using "Successive Flowering" as the dependent variable and "First Flowering" as the independent variable, indicated a highly significant relationship. The value for "b", the slope, in the regression equation was 0.468, meaning that approximately half of the trees flowered in the year succeeding their initial flowering. This would indicate that the early precocious flowerings need not be considered a freak of nature, but an indication that the so-called non-sexual cycle of these trees has been completed and that they are able to continue to produce functional reproductive structures.

Effect of geographic seed source: Jack pine seedlings not only flower at a very early age (2 years), but also produce numerous flowers of both sexes. From a statistical analysis of the number of male and female flowers on 4-year-old trees in a geographic seed source test, it became quite apparent that the seed source has a highly significant effect on the number of trees that flower, and on the number of flowers per tree. The trees under observation originated from seed collected in St. Louis, Pine, and Itasca Counties in Minnesota; and Wood and Oneida Counties in Wisconsin. The trees were obtained from the Lake States Forest and Range Experiment Station of the United States Forest Service and were outplanted at Norfolk, Connecticut. The field design consisted of a randomized block layout with 6 replications. A X^2 test on the number of trees that flowered indicated that the origin of the seed significantly (1% level) affected the number of trees that flowered. Using the "New multiple range test" by Duncan (1955) with the error term from an analysis of variance on the transformed data, the trees from Pine County, Minnesota showed both a significantly smaller percentage of trees that flowered, as well as a smaller number of flowers per tree. This seed source was less than 150 miles from its adjacent source, indicating that there are local ecotypes within the natural range of Jack pine that, when grown under Connecticut conditions, have a shorter interval from seed germination to flower production that is genetically controlled.

Effect of hybridization: From observations in our progeny testing plantations it is quite apparent that interspecific hybrids from both the Haploxylon and Diploxylon group flower occassionally at an earlier age than seedlings from either parents. It is possible that complementary genes present in the parental species shorten the juvenile non-reproductive stage. In addition, by interspecific hybridization genes from early flowering species can be introduced into those flowering later.

Attempts to stimulate flowers by altering the physical environment: Experiment A) Two year-old seedlings of sand pine received three levels of chilling treatments during the summer and early fall. The treatments were ineffective in stimulating flowering, but the seedlings that were treated in the late fall grew most vigorously in the following growing season.

Experiment B) Seedlings of Scotch pine and Norway spruce were subjected to a photoperiod of 16 hours in a greenhouse during two growing seasons. The seed had been collected from four geographic locations, and the seedlings were 8 months old when they were moved into the greenhouse. In this experiment combinations of photoperiod, temperature, and cold treatment were evaluated. At the conclusion of the study after two additional growing seasons, several of the pine seedlings that had received cold treatments and were subjected to a 16-hour-light period in the greenhouse produced male or female flowers. The flowering was too erratic, however, to make any type of statistical analysis, but the seedlings that flowered were the most vigorous ones. Experiment C) Using a randomized split plot design, one-year-old Scotch pine, seedlings from five geographic sources were placed under four light intensities in a greenhouse and in the field. The light conditions were: full light, 25% of normal light, 10% of normal light, and 2% of normal light. The reduced light conditions were obtained by placing the potted seedlings in cages that were covered with layers of cloth. It should be pointed out that this treatment also affected the temperature and humidity conditions within these cages.

The results on flowering in this experiment were opposite to those of the study reported previously. The treatment that stunted the growth to the greatest extent, namely location under 10% of 2% of normal light intensity in the greenhouse without cold treatment, were the only treatments that stimulated male flowers. Using an exact statistical test on the data, the effect on flowering was significant at the 3% level. Of interest also was the fact that the male catkins matured during July, whereas older *Pinus sylvestris* trees in the vicinity of the greenhouse flowered in mid-May. The catkins on the seedlings were abnormal, were spherical in shape, and had the appearance of male flowers of *Taxus*. Possibly because of the stunted growth of the seedlings, this group had the highest nitrogen content (2.5%), as compared to the controls that had 1.9% O.D.W. basis. The most prolific flowering occurred on the most stunted seedlings and on seedlings from the northern sources (Inari, and Rovaniemi, Finland, and Tonset, Norway).

Experiment D) Mirov (1939) was able to stimulate flowering in five species of pine by inarching one-year-old seedlings into the crown of a mature, flower-bearing tree. Two years after grafting, male flowers were produced on all species but slash pine, *Pinus elliottii* Engelm. I repeated a similar study without success. Seedlings were inarched into various positions in the crown of older slash pine trees, but during the three years that they were under observation, they maintained their juvenile appearance and none of them produced flowers.

Treatment with liquid fertilizer, high temperature and high humidity: From the evidence in the literature on time of initiation of flower primordia in members of the Diploxylon group, some of the primordia apparently are not laid down in the growing season prior to their anthesis, but during late winter or early spring before they appear. In a recent study by Stephens (1961) he was able to observe male strobili in white pine in the fall preceding flowering, but he was unable to locate female flowers until the spring preceding flowering. Therefore, members of this group are suited for experiments to obtain responses to treatments within a relatively short period.

Dormant 18 month-old potted seedlings of eastern white pine, *Pinus strobus* L., and *Pinus griffithii* McClelland x *Pinus strobus* hybrids were subjected to a sudden change in temperature and humidity by placing them into a 21°C. greenhouse during the beginning of January. As soon as the soil in the pots had thawed, the plants were watered with a liberal dose of a 1/2% aqueous solution of a 12-12-12 liquid fertilizer. After a short adjustment period the seedlings responded rapidly and normal growth started, and after seven-weeks in the greenhouse rudimentary male and female flowers appeared on the *Pinus griffithii* x *Pinus strobus* seedlings. Of a total of 156 seedlings in the greenhouse, 15 trees had flowers, while none of the controls produced flowers. Because none of the *Pinus strobus* nor *Pinus griffithii* seedlings produced flowers, this flowering was probably caused by a combination of the shock treatment, and the effect of interspecific hybridization. As in the other instances, the pollen of the male catkins was viable, and the female strobili appeared normal. Female strobili that were not pollinated or that were selfed, withered and fell off during the early part of the summer; those that were cross-pollinated continued normal development.

Needle samples for N determination were collected from the flowering seedlings as close to the locus of flowering as possible; needles from the new growth were not taken. For the controls, needles were selected from similar locations on non-flowering seedlings. The C/N ratios of the needles were the same for both the flowering and non-flowering seedlings (72.186 vs. 72.814).

Effect of Physical and chemical treatment: In a randomized 2 x 2 x 2 factorial experiment the effects of root-pruning, stem injury and fertilization were evaluated on 3-year-old *Pinus clause* seedlings that were growing in a greenhouse. The treatments were started during June and continued over a period of one year. For the root-pruning, one half of the roots were removed and the trees were placed back in the original pot. Aluminum foil was placed along the edge of the cut surface to prevent the roots from growing into the other part of the flower pot. For the stem injury a 2 cm wide girdle (bark and cambium) were removed, leaving about one quarter of the stem intect. The fertilized trees received at weekly intervals 100 cc of an aqueous solution of a 12-12-12 soluble fertilizer.

Observations on flowering were made during a period of two years, and although a considerable number of trees flowered (43/96), there was no relationship between treatment and the production of reproductive structures. Flowering was distributed randomly among the seedlings and both male and female flowers were produced in abundance.

At monthly intervals during the first year after treatment, needle samples were collected from each tree to determine the O.D.W., and the content of nitrogen. The purpose of these analyses was to see whether there was a relationship between flowering and a specific C/N ratio, or whether flowering was associated with a change in the ratio during the period while flower initiation took place. For the analysis the individual tree data were plotted, along with indicator lines of the approximate C/N ratioes. In this experiment flowers were produced in trees with ratios varying between 1.0 and 1.7, and in absolute amounts of N varying by a factor of 2.

Various graphs were prepared of the changes in C/N that took place during the spring and summer when flowers were initiated. The differences in C/N ratio between July 15 and August 14, or during the time when flower primordia initiation took place were plotted and it became quite obvious from this graph that flower production and a change in C/N ratio, (either positive or negative), were not associated.

General

In our greenhouse I have a fairly large number of slash pine, loblolly pine, and longleaf pine seedlings. These seedlings are kept under a high level of N fertilization. As a result of this treatment flowering is quite common amongst three-year-old slash and loblolly pine, and this past spring we had 8 longleaf pines out of a total of that produced female flowers while they were still in the grass-stage. In addition, some seedlings flowered during the first year after they started height growth.

There is an interesting phenomenon associated with high N fertilization. Already when Hoekstra and myself worked on the stimulation of flowers in slash pine we noticed an increase in the number of hermaphroditic male flowers that were produced as a result of fertilization (Hoekstra and Mergen, 1957). In a recent study on the induction of flowers in young white pine hybrids, I observed a similar phenomenon. A large number of the male flowers were hermaphroditic, and the upper part of the strobili had changed into female structures. Germination of pollen collected from these hermaphroditic flowers germinated normally *in vitro*, and the sex inversion was complete in some instances so that viable seed was obtained after pollination.

DISCUSSION

From the results presented one can conclude that, 1) the ability to flower at an early age is genetically controlled, and 2) in flowering trees the mechanism that controls the change from a vegetative shoot to a sexual one can be modified to some extent by the environment. As in any other growth phenomenon, the resultant is the product of the interaction of a particular genotype with its environment. It appears that in certain species the degree of genetic control of the juvenile period is more plastic and therefore these species lend themselves better to manipulative flower induction techniques.

The results of studies by previous investigators, as well as those reported by me, are of little help in explaining the biochemical and physiological changes that bring about early flowering in trees. Neither do they throw any light on the various theories that try to explain flowering. The question of whether early flowering is induced by an excess of auxin or by a lack of auxin is still unanswered. The majority of the successful techniques rely on changing the C/N ratio, with the concentration of nitrogenous compounds being affected to the greatest extent. What effect this has on shortening the juvenile stage is not known, nor can a specific C/N ratio, or even a range of ratios, be assigned as an index of when the change from vegetative growth to reproductive growth will take place. A particular ratio will not give the absolute amounts of its two variables, and a wide range of conditions can give the same ratio.

To check on some of the theories, and to analyze chemically the experimental material, we need to find manipulative techniques that are reliable, and that can be repeated over a period of years by investigators in various parts of the world. Environmental changes, although quite effective and important, need to be backed up by studies that check the correlated modifications. To find reliable techniques, a great deal of empirical work needs to be done, such as testing the effects of certain treatments under very uniform conditions. With the current popularity of controlled light and temperature rooms, it should be much easier to carry out these studies. It is also important that information on failures and successes be exchanged even if the results are not too striking.

The entire field of cell differentiation, of which juvenility is a part, is a fascinating one that has challenged the ingenuity of researchers for quite some time. It is one of the most basic areas in biology, and needs to be explored cooperatively by the biophysicists, the enzyme chemists, and the physiologists, and the botanists.

Summary

In summarizing, I would like to mention that: 1) Mugo pine seedlings have flowered when less than one year old and before they had produced secondary needles, 2) once a tree has begun to flower, it can continue to do so, 3) there is evidence that within *Pinus banksiana* some geographic ecotypes are more precocious than others, 4) interspecific hybrids flower occassionally at an earlier age than the parent species, 5) flower induction may be stimulated in two-year-old *Pinus sylvestris* seedlings by either severe retardation or stimulation of growth, and 6) treatment with a 12-12-12 fertilizer along with a temperature and humidity shock, induced male and female flowers on *Pinus griffithii x Pinus strobus* hybrids that were less than two years old.

Literature Cited

Duncan, D. B. 1955. Multiple range and multiple F tests. Biometrics 2: 1-42.

Hoekstra, P. E., and F. Mergen. 1957. Experimental induction of female flowers on young slash pine. Jour. For. 55: 827-831.

Mergen, F., and S. G. Cutting. 1957. Male flowers on one-year-old Mugo pine seedlings. For. Science 3: 355-356.

Mirov, N. T. 1951. Inducing early production of pine pollen. U.S.D.A., Cal. For. and Range Exp. Station, For. Res. Note 80: 3 pp.

Stephens, G. R., Jr. 1961. Flower induction in woody plants. Ph. D. dissertation. Yale University. 75 pp.

Righter, F. I. 1939. Early flower production among the pines. Jour. For. 37: 935 - 938.

Wareing, P. F. 1953. Experimental induction of male cones in Pinus sylvestris. Nature 171: page 147.

CONE AND SEED INSECTS AND THEIR CONTROL

by

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At the Lake City Research Center we have been concerned mainly with the identification of insects affecting the seed production of slash and longleaf pines and the chemical control of the most destructive species on slash pine. Two groups of moths, the Dioryctria coneworms and the Laspeyresia seedworms, have been found to be the most serious pests of cones and seeds. A thrips, Gnophothrips piniphilus Cwfd., has also been found to kill and seriously injure the succulent flowers.

At least two other groups of insects attack the cones. These are flies of the family Itonididae (Cecidomyiidae) and scale insects of the Toumeyella, or tortoise shell group. The larvae of the flies kill cones, or parts of cones, by feeding between the cone scales. These insects are not common on cones in northeast Florida. The scales attack cone stalks, but usually only a few individuals develop on any one stalk. Several predators and at least one parasite appear to be quite effective in reducing the number of scales reaching maturity so that an infestation seldom affects the development of the host cones.

We shall devote the remainder of our discussion to the biology and control of the three groups of insects which we consider to be the most destructive: the coneworms, the seedowrms, and the flower thrips.

THE PINE CONEWORMS

Three species of Dioryctria coneworms, the most omnivorous of the flower and cone insects of southern pines, are common in north Florida. As a group they attack flower buds, vegetative buds and growing tips (including flower-bearing shoots), and both first- and second-year cones. They are also common in conelets infected with cone rust, in fusiform rust cankers, and in both injured and apparently healthy tree stems. Each species produces several generations per year.

All studies on the chemical control of Dioryctria spp. at Lake City have been concerned with the protection of slash pine seed crops. In our tests we have used only high-pressure hydraulic sprays to apply insecticides to trees ranging in height from 30 to 50 feet. These tests were designed to determine whether or not we can obtain good control with equipment that will give high-volume sprays with complete, or nearly complete, spray coverage. After this type of equipment has been thoroughly tested, we can study the effectiveness of mist-blower and aerial application.

During the past 2 years a 0.5-percent gamma BHC water emulsion was applied in two spray schedules for *Dioryctria* control. One schedule consisted of sprays applied every other month. The dates arbitrarily chosen were February 20, April 20, June 20, and August 20; applications were made in 1959 and 1960. The other schedule was based on our present knowledge of the biology of the three coneworm species. This biologically timed spray schedule consisted of four applications in 1959; i.e., on February 24, April 7, May 29, and June 26. In 1960, the biologically timed sprays were applied only three times, on March 29, June 1, and July 30. The February application was dropped because it was found that coneworm attacks during the winter and early spring were very light.

Both the arbitrary and biologically-timed spray schedules gave 95 percent or better protection to first- and second-year cones in 1959 and 1960. It appears, therefore, that precise timing of sprays may not be too essential for coneworm control. Based on our research to date, we are recommending hydraulic spray applications of 0.5-percent gamma BHC water emulsion for *Dioryctria* control as follows: (1) first application from mid- to late April; (2) second application from late May to early June: and (3) the last application from mid- to late July.

In 1959 and 1960 a 0.5-percent BHC emulsion was also applied on a special schedule for *Laspeyresia* control. In 1959, two applications, on May 4 and May 19, failed to control seedworms, but the protection from *Dioryctria* attacks were just as good as that obtained with the two coneworm spray schedules already discussed. In 1960, the BHC applications were increased to five between April 11 and June 1. Here again, as in 1959, no seedworm control was obtained, but *Dioryctria* control was excellent. These experiments bring out two points concerning the chemical control of *Dioryctria* spp. One is that the applications of BHC during the period from early April to early June appear to be most important for good control. Secondly, the results of the two May sprays in 1959 indicate that as few as two applications can give good coneworm control. Both of these hypotheses are being investigated.

THE PINE SEEDWORMS

Although *Laspeyresia ingens* Heinrich and *Laspeyresia anaranjada* Miller infest slash pine cones, *L. anaranjada* is by far the more common of the two species in north Florida. The female moth of *L. anaranjada* lays eggs on second-year cones only, from early to mid-May, and produces a single generation each year. The larva feeds within the developing seeds until cones mature. After normal seed fall, larvae bore into and overwinter in the cone axis. Pupation also occurs in the cone axis galleries and moths emerge through seeds which have been hollowed out the previous year. Generally, 1 to 3 larvae are found per cone and each larva destroys 5 to 7 seeds. There is no external evidence of seedworm infestation before cones mature, and because damaged seeds are retained in the cones after normal seed fall, cones must be cut open to evaluate seed losses accurately.

At Olustee, Florida, last year, a 49-percent sample, or 1,822 cones, were examined from the total cone crop on 28 slash pines. After bisecting the cones we found that 73 percent were infested by *L. anaranjada*. The estimated number of seeds destroyed by larvae was 10 percent of the potential, sound, full-seed yield of both infested and uninfested cones. The interesting point, here, is that the actual seed loss was considerably less than one might expect from the high percentage of infested cones. Percent cones infested, by itself, is not a good index of seed losses because seed loss is more dependent on the number of larvae per cone than on the number of cones infested.

The losses, just cited, were determined in an area containing open-grown pines which simulated seed orchard conditions. This single example may or may not be representative of the losses that might be caused by this insect in future seed orchards, but it does indicate the potential destructiveness of the species.

As mentioned earlier, the 0.5-percent BHC water emulsion failed to control *Laspeyresia anaranjada* in 1959 and 1960. Exploratory research in 1960 showed Guthion to be a very promising insecticide for seedworm control. Laboratory insecticide screening tests have shown that Guthion is also highly toxic to mature *Diorcyctria abietella* larvae. A word of caution, Guthion is highly toxic to humans as well. As a result of these studies we are presently conducting field experiments to determine whether Guthion treatments can be devised which will control seedworms and coneworms at the same time.

One interesting possibility for the control of seedworms in seed orchards lies in the complete removal of the total mature cone crop each year. Since the seedworm larvae are in the cones at harvest time, it might be possible to remove the entire seedworm population. The effectiveness of such a cultural control method would depend on: (1) the thoroughness of the cone collections each fall; and (2) the ability of Laspeyresia moths to reinvade seed orchards.

THE PINE FLOWER THRIPS

The pine flower thrips, Gnophothrips piniphilus, is a small (1/16-inch long), slender black insect which appears on and around developing female flower buds early in January as the twig bud stage becomes obvious on slash pine terminals. These thrips feed externally until the buds begin to unfurl. They then attack the tender flower parts and continue feeding until shortly after pollination is complete. Injury is first noticeable when excessive resinosis, in the form of beaded droplets, appears on the flowers. Some severely attacked flowers shrivel and die, others die as young conelets, and still others produce deformed cones because of the death of part of the cone scales.

An exploratory study for the control of this thrips was conducted in 1960. Several insecticides were used as recommended for thrips control on agricultural crops. From this study heptachlor was selected as the most likely material for further tests.

In 1961, heptachlor was applied as a 0.1 percent water emulsion spray to individual flower clusters. Two spray schedules were followed. In one the flower clusters were sprayed only when in early stages; i.e., twig bud stage through stage 1 of flower development. In the other schedule flower clusters were sprayed both in early and nearly mature (2 through 2+) stages of flower development. Reduction in flower attacks by thrips was highly significant for both spray schedules. No significant difference occurred between the two schedules.

Complete tree spraying with .05-percent water emulsion of heptachlor was also tested. This spray was applied by a hydraulic sprayer to flowers in both early and later stages of development. It was combined with a fermate spray schedule set up by the Division of Forest Disease Research for the control of cone rust. Control of thrips injury by this spray schedule was highly significant. Attacks recorded on about 1,500 sprayed flowers averaged only 4.7 percent as compared to 33.9 percent on a similar number of check flowers.

Although the pine flowers showed no obvious injury from the heptachlor or combination sprays, the yield and viability of seed from sprayed and unsprayed cones will be compared to determine if the sprays interfered with normal flower fertilization.

SUMMARY

A summary of our progress in the chemical control of slash pine cone and seed insects is as follows:

1. Hydraulic spray applications of 0.5-percent gamma BHC water emulsion have effectively controlled Dioryctria spp., the most destructive group of insects affecting slash pine seed production. Research is continuing on the minimum number of sprays necessary for adequate cone protection. Tentative spray recommendations have been presented.

2. The 0.5 percent BHC emulsion failed to control *Laspeyresia anaranjada.* Guthion shows promise for the control of this pest.

3. Control of the flower thrips with heptachlor was significant in 1960 and 1961.

INTERRELATIONSHIP OF WOOD PROPERTIES OF LOBLOLLY PINE

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Within the short span of less than a decade, interest has burgeoned remarkably fast around genetic control of certain wood properties. In line with this manifestation research has been initiated to determine the degree of genetic influence on specific gravity, summer wood per cent, tracheid length, cell wall thickness, cell diameter, fibril angle, cellulose yields, per cent lignin, and other characteristics. In most instances each characteristic has been studied by itself, ignoring possible interrelationships among the variable properties; study of several characteristics jointly has been rare. Now it seems clear that if really meaningful results regarding genetic control of wood are to be achieved, it is necessary to determine whether characteristics are wholly independent, or whether several are so closely interrelated that if some are changed, the others will change also. Effective progress through the application of genetic principles is unquestionably dependent to a very large degree on the nature and extent of interrelationships existing between different characteristics. Failure or neglect to recognize such interrelationships where they exist could well render breeding programs ineffective or inconsequential.

Although the present paper does not deal in genetics per se, nor in actual inheritance patterns of various wood properties, it does represent an exploration of possible interrelationships in several important wood characteristics. Supporting data obtained from both genetic and non-genetic wood studies[1] will center on characteristics largely of loblolly pine.

This paper will be divided into two parts, namely, (1) a report of interrelationships of four wood characteristics (both for core and outer wood) on 14 loblolly pine trees selected from lands of the Riegel Paper Corporation for use in their seed orchard, and (2) data from wood studies of the trees used in the Industry seed orchards. Wood property interrelationships both within individual trees and among large numbers of trees from a 10-state area will be emphasized.

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[1] Most of the data obtained were from joint college-industry studies of trees used in the N. C. State-Industry Forest Tree Improvement Program.

What Is a Wood Property?

First, let us be sure we all understand what is meant by a wood property. Some "properties" are clean and easily defined; thus, tracheid length is unambiguous, and the only qualification needed is to designate "where" it is being measured. On the other hand, specific gravity, although commonly referred to as a wood property, must at least from a growth or genetic standpoint be considered as a complex of characters that may or may not closely interrelate to other specific characters, singly or in combination. Thus, even though specific gravity, per se, can be specifically defined and is relatively easy to measure, genetically it is essentially not an element but a compound. As stated by Schreiner (Zobel, 1956) "The genetics of specific gravity is a complicated problem--I have indicated earlier that it is an oversimplification to say that specific gravity of wood is inheritable. Specific gravity is obviously not controlled by a single hereditary factor. The length and diameter of the wood cells, thickness of the cell walls, proportion of springwood and summerwood, per cent of cellulose and lignin, and composition and amount of other chemical constituents of the wood, are some of the wood characteristics that--probably determine wood specific gravity. In respect to these wood characters, it is possible: (1) that they may be controlled by individual genetic factors; (2) that two or more may be under the control of a single factor; (3) that some, such as per cent of summerwood, may depend on more than one genetic factor; (4) that some may linked, i.e., transmitted as a unit from parent to offspring--specific gravity is therefore the final expression of the effect of environmental factors on the inheritable potential of the tree to produce wood with a number of particular characters."

Schreiner has appropriately and succinctly emphasized the complex involvement of specific gravity in the genetics picture. Nevertheless, despite widespread recognition of this complexity, specific gravity is usually still regarded and handled as a unit wood characteristic. It will be so handled here, again, but not without the preceding preface to warn of these complexities. It is also well to keep in mind that numerous other characteristics of wood may be as complex as specific gravity.

RELATIONS OF FOUR WOOD CHARACTERISTICS OF LOBLOLLY PINE

For all trees used in the seed orchard of the Riegel Paper Corporation, determinations were made of the following wood characteristics in an effort to ascertain the worth of each selection: (1) specific gravity, (2) tracheid diameter, (3) tracheid length, (4) tracheid wall thickness, (5) cellulose, termed WRC[1], and (6) alphacellulose.

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[1] Stands for Water Resistant Carbohydrates, similar to holocellulose.

By means of the large (10 mm) increment borer, wood samples were extracted from the bole of the tree at the breast height position, i.e., 4.5 feet above the general level of the ground. These increment cores were then divided into two sections: (l) the first 7 rings from the pith (referred to as core wood, and (2) the remainder of the core from the 8th ring out to the cambium (referred to as outer wood). All trees sampled were excellent phenotypes and were the fastest growing, dominants in the stand. Six of the trees were from the North Carolina Coastal Plain, the remaining eight from the North Carolina Piedmont. All were young, vigorous trees averaging 34 years in age, 11.8" in diameter, and 70 feet in height.

Specific gravity, tracheid lengths, and cellulose were determined separately of each setment of each increment core; i.e., the core segment comprising the first 7 rings was handled and pulped as a unit, and similarly the outer wood from the 8th ring was treated as a unit. Maceration techniques and measurement methods were similar to those we normally use (Zobel, et al, 1960) with one major exception: all tracheids, whether whole or cut were measured so the average lengths will be less than for the whole tracheids only reported later in this paper. Length, width, and wall thickness data are based on 50 to 70 tracheids per core segment. Measurements of the tracheid characteristics were made for the Riegel Paper Corporation at the Institute of Paper Chemistry, Appleton, Wisconsin, while specific gravity and cellulose determinations were made at the School of Forestry, N. C. State College.

Both core and outer wood values are shown in Table 1. We shall examine these data from three directions, namely, (1) variation from tree to tree for each characteristic; (2) strength of the correlations of core to outer wood values; and, (3) interrelationships of wood characteristics among trees.

1. Variation from tree to tree.

For all four characteristics shown in Table 1, individual tree variation is impressively large; it can be noted here that variation also is equally large for cellulose values. For convenience, the data showing means and range have been consolidated in Table 2. The variation in tracheid lengths is less than that usually reported, but this outcome is not surprising since both cut and uncut tracheid measurements are included in this data. Inclusion of cut tracheids results invariably in a reduction in the percentage of the long tracheids which suffer disproportionately in the maceration treatment. Published data on cut tracheid lengths always show less tree-to-tree variation than is found when only whole, uncut tracheids are used.

Table 1. Wood properties of trees used in the Riegel seed orchard. The "core" portion consists of rings #1 through #7 counting from the pith; the "outer" portion is from ring #8 outward. All samples taken at breast height (4.5 feet above the base of tree).

Tree No.	Tracheid Length[1] Millimeters		Tracheid Width Millimeters		Wall Thickness Microns		Specific Gravity	
	Core	Outer	Core	Outer	Core	Outer	Core	Outer
9-2	2.63	3.73	.050	.049	5.16	7.69	.42	.55
9-3	2.28	3.58	.049	.046	4.82	9.49	.49	.58
9-4	1.64	2.81	.042	.049	3.39	4.44	.42	.49
9-5	1.44	3.26	.045	.046	3.53	6.46	.39	.46
9-6	2.00	3.30	.044	.047	3.92	6.20	.51	.61
9-7	2.30	3.54	.045	.053	3.59	5.61	.39	.50
9-9	1.89	3.76	.047	.050	2.82	6.94	.46	.52
9-10	1.84	3.67	.046	.056	3.67	6.81	.42	.52
9-12	2.49	3.55	.055	.050	4.81	7.84	.47	.59
9-14	2.28	3.86	.046	.053	4.22	6.30	.46	.49
9-15	2.02	3.88	.047	.051	4.14	6.84	.44	.50
9-16	2.13	3.83	.049	.061	4.19	5.85	.42	.43
9-17	2.02	3.56	.048	.054	4.07	6.94	.46	.52
9-18	1.82	2.86	.047	.052	3.90	5.62	.43	.51
Averages	2.06	3.51	.047	.051	4.02	6.65	.44	.52

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[1] Tracheid lengths consist of measurements of both cut and uncut tracheids. Each value represents average of measurements on 50 to 70 tracheids.

Table 2. Averages and range of values for wood characteristics in the core wood and in the outer wood of some loblolly pine trees used in the Riegel seed orchard.

Characteristic	Core Ave.	Outer Ave.	Core Range	Outer Range
Specific Gravity	.44	.52	.39 - .51	.43 - .61
Tracheid Length (mm)	2.06	3.51	1.4 - 2.7	2.8 - 3.9
Wall Thickness (microns)	4.02	6.65	2.8 - 5.2	4.4 - 9.5
Tracheid Width (mm)	.047	.051	.042 - .055	.046 - .061
WRC	--	79.3	---	77.5 - 80.5
Alpha Cellulose	--	57.0	---	54.1 - 59.6

The observed individual tree variation is very encouraging to the geneticist; here it is of sufficient magnitude to indicate considerable chances for improvement. Having found this variability, his main job is to unearth the causes of the individual tree variation and to determine whether, or how much of, it is genetically controlled.

2. Relationship of Characteristics of the Core Wood to Outer Wood.

The strength of relationship of a wood characteristic near the center of the tree (core wood) to the same characteristic further from the tree center, (i.e., in the outer wood) is of a great deal of interest and importance. Although a complete literature review will not be made here, attention is called to a number of studies such as the ones by Kramer (1957), Jackson (1959), and Zobel & Rhodes (1955), in which the magnitude of relationships that might be expected for specific gravity and tracheid length have been indicated; these items will be discussed in considerable detail in the next section. It should be noted here, however, that even though the present data are based only on 14 trees, significant correlation coefficients of .55 and .54 were obtained respectively for the core and outer specific gravities and core and outer tracheid lengths. These coefficients are quite in line with other published data.

Of special interest here, however, is the relationship between values for tracheid width and tracheid wall thickness for the core and outer wood samples, since previously published data for these characters are not available. As illustrated in Fig. 1, there is a statistically significant relationship in wall thickness between the first (core) and later formed wood having an "r" value of +0.61. In contrast to this finding about wall thickness, no significant relationship was found for tracheid width between the core and outer wood (Fig. 2). Lack of significance here would indicate that the tendency for development of thicker-walled tracheids shows up early in the life of the tree, while tracheid width, which often has considerable variation between the radial and tangential dimensions, has shown no relationship in the present study. Certainly better-designed examinations, including more trees, must be made before definite conclusions about tracheid width correlations can be made. However, judged from the present, though rather inadequte, data, it would appear that the trees with larger diameter tracheids at maturity do not necessarily have very wide tracheids near the pith.

The tracheids of outer wood are about 1.5 mm longer than those in the core wood; walls of outer wood tracheids are 2.6 microns thicker than those of the core wood; specific gravity of the outer wood is substantially (.08) higher than core wood; tracheid width of outer wood averages only slightly greater than core wood indicating that at least on these 14 trees the change isn't great from pith to bark.

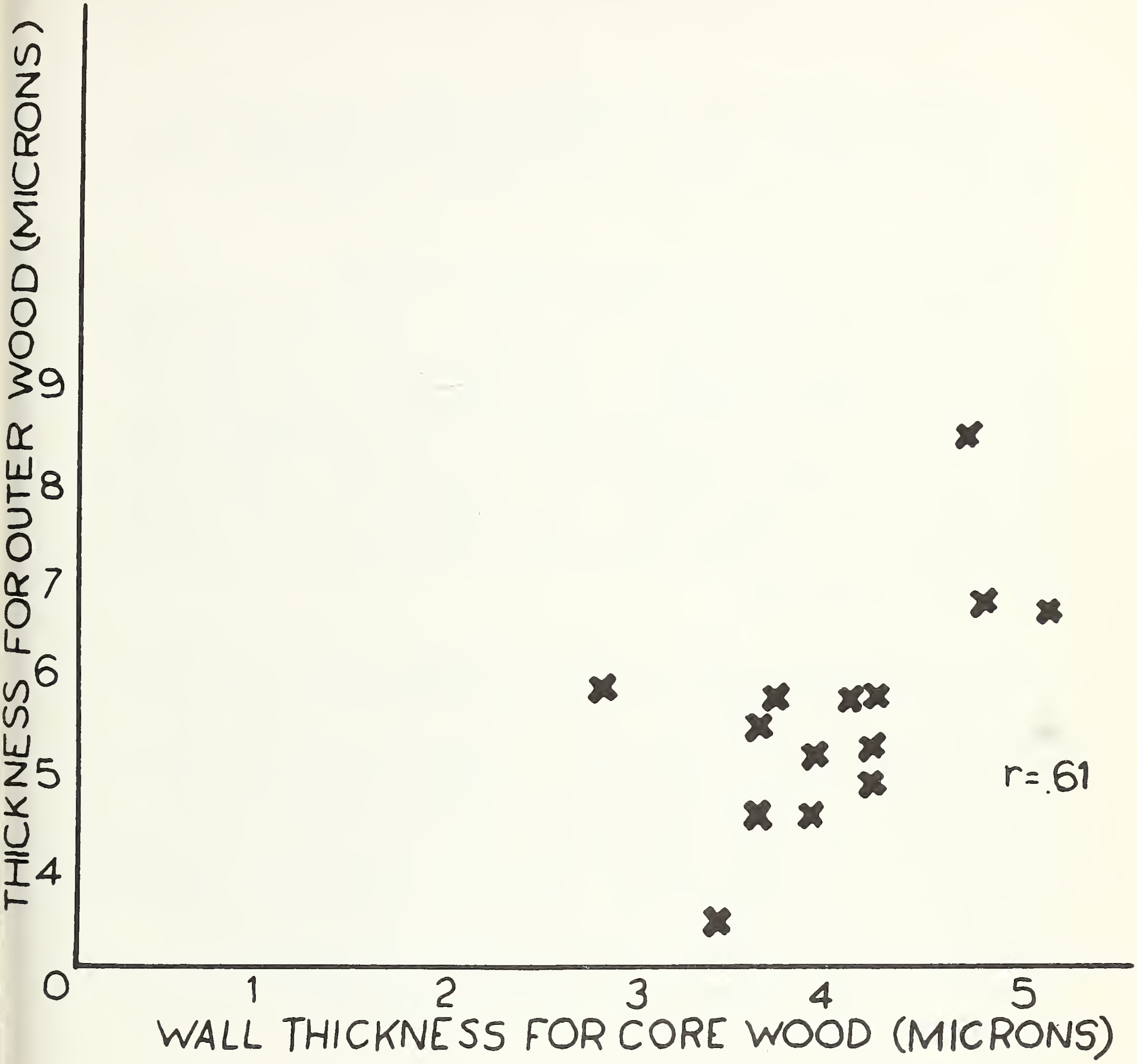

Figure 1. Graph showing the statistically significant correlation found in tracheid wall thickness between core wood and outer wood.

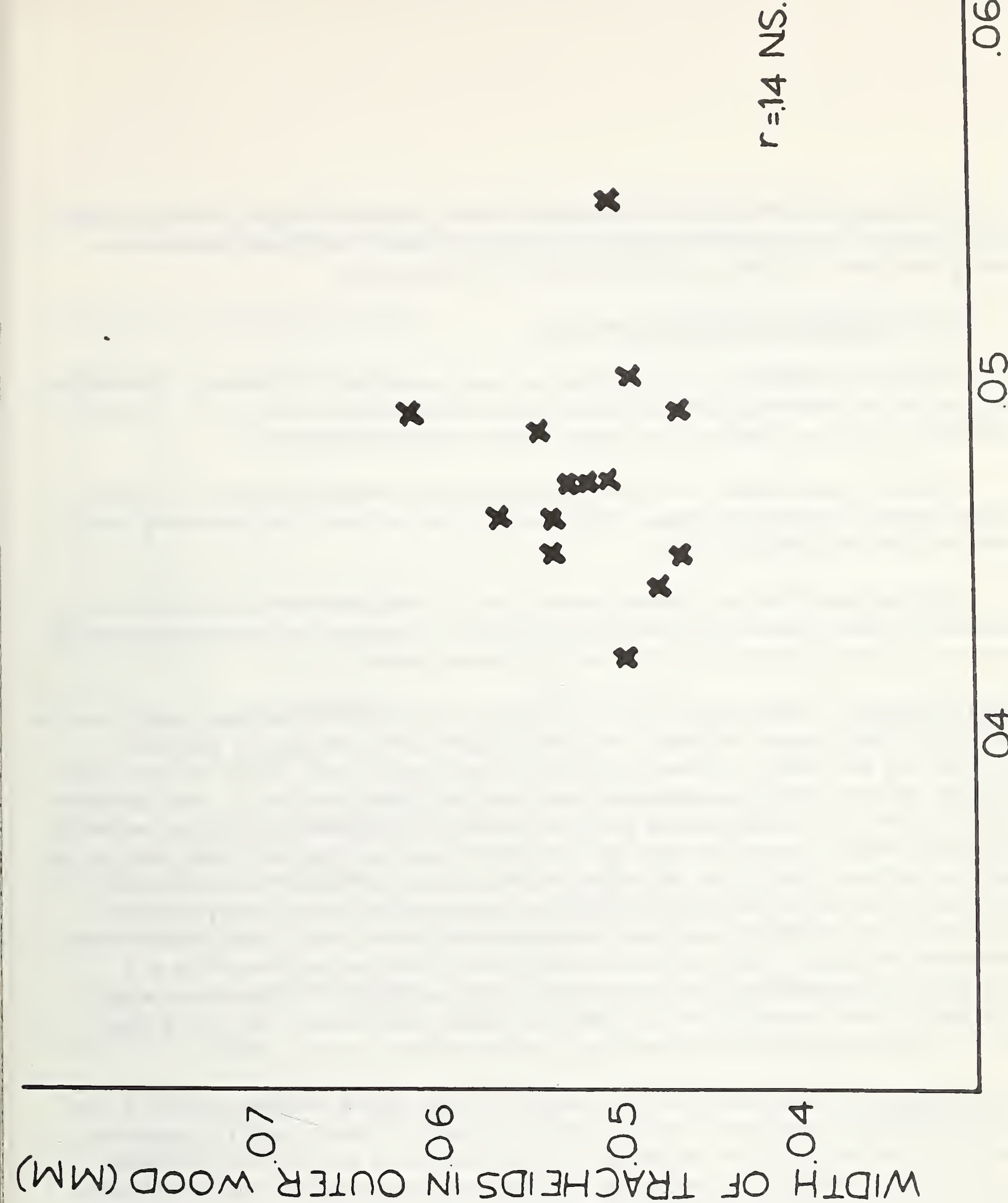

Figure 2. Graph Showing the lack of statistical significance found for tracheid width between core wood and outer wood.

In summary, then, it was found that specific gravity, tracheid length, and wall thickness of the wood formed in the first 7 rings from the pith are indicative of these characteristics during later years. Tracheid width did not show this relationship.

3. Interrelationships of Wood Characteristics.

To make the desired progress in breeding for wood properties, it is necessary to determine whether various properties in which interest is centered are interdependent, i.e., they are inherited as a unit, or does each one change without affecting the other.

A number of correlations were calculated among the six wood properties for the Riegel Paper Corporation seed orchard trees. Relationships shown in Table 3 include simple correlations for WRC and alpha cellulose.

Partly because of the small sample number, (only 14 trees) none of the correlation coefficients in Table 3 were highly statistically significant. However, the coefficients indicate some very interesting trends, as will be briefly discussed below.

Specific Gravity: There appears to be a slight trend indicating that the higher specific gravity trees have slightly shorter tracheids. This trend is quite weak in the present study with r = -.30 as it was found in another recent study (Zobel et al., 1960), where "r" was -.162. However, because of the large number of trees involved in the latter, the "r" was significant at the 1% level, but though specific gravity accounted for only about 2.5% of the variability in tracheid length. Trees with higher specific gravity might be expected to have more narrow cells, as was found here. Also, the higher specific gravity trees have thicker cell walls. For several previous studies we reported that the higher specific gravity trees yielded less WRC per unit dry weight of wood than the lower specific gravity trees, while in other studies the reverse was found. Thus, the picture on WRC is confusing and not susceptible to a satisfactory interpretation at this time; however, alpha-cellulose yields seem to be slightly to strongly related to specific gravity of the wood (Zobel & McElwee, 1958) unless these earlier results simply reflect some peculiarity in the method of analysis used.

Tracheid Length: There appears to be a trend for the trees that have longer tracheid to also have thicker walls and also to have higher cellulose yields, although again the correlation coefficients failed to reach an acceptable level of significance with the small number of trees involved. It might be expected that the larger diameter tracheids would have thicker walls, but it is difficult to reason why they should have higher cellulose yields, unless again it is a reflection of the method of cellulose determination.

Table 3. Correlation coefficients of several wood and growth characteristics for 14 loblolly pines, outer wood only for trees used in the Riegel seed orchard.

Relationship of Wood Characteristics	Correlation Coefficient
Specific gravity x tracheid length	-.30 NS
" " x tracheid width	-.58*
" " x wall thickness	.56*
" " x WRC[1]	-.35 NS
" " x alpha-cellulose	.24 NS
Tracheid length x tracheid width	.44NS
" " x wall thickness	.49 NS
" " x WRC	.12 NS
" " x alpha-cellulose	.04 NS
Tracheid width x wall thickness	.32 NS
" " x WRC	.48 NS
" " x alpha-cellulose	.39 NS
Wall thickness x WRC	.56*
" " x alpha-cellulose	-.15 NS
WRC x alpha-cellulose	.56*

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[1] Water resistant carbohydrates, similar to holocellulose.
* Significant at the 5% level.
NS Not statistically significant.

Correlation of Several Characteristics: No multiple correlations were calculated for this study, but a rough ranking was made to show the relative position of each of the 4 tracheid characteristics for each tree. When making this ranking, one fact immediately becomes evident; i.e., that most of these characteristics seem to be present in any one tree in a rather random manner without particular relationship to the other. This indication, of course, is reflected in the magnitude of the correlation coefficients. For example, we have high specific gravity trees with long tracheids and narrow cells, as well as with short tracheids and wide cells. Nearly all such combinations were found in the 14 trees studied. For purposes of illustration, eight of the trees so ranked are shown in Table 4, below. Four of these are shown graphically in Figure 3.

Table 4. Ranking of selected trees by four characteristics. The numbers indicate relative positions in the order of the 14 trees studied, the higher numbers indicating high specific gravity, long tracheids, wide tracheids, and thick-walled tracheids; the low numbers indicating low, short, narrow, and thin-walled, respectively.

Relative Rankings - From 1 to 14

Tree #	Total Points	Specific Gravity	Tracheid Length	Tracheid Width	Wall Thickness	Classification			
						Sp.Gr.	Length	Width	Wall Thckness
3	35	12	8	1	14	high	inter.	narrow	thick
4	9	3	1	4	1	low	short	narrow	thin
6	28	14	4	3	7	high	short	narrow	inter.
9	36	9	11	6	10	inter	long	inter.	inter.
10	40	10	9	13	8	high	inter	wide	inter.
12	38	13	6	6	13	high	inter	inter	thick
15	36	5	14	8	9	low	long	inter	inter.
16	31	1	12	14	4	low	long	wide	thin

From Table 4 it is obvious that we have trees with many combinations of wood characteristics such as high specific gravity with short, narrow, intermediate-walled cells, or of high specific gravity, intermediate tracheid length with narrow, thick-walled cells. These results are encouraging to the geneticist because they indicate that intensive selection for specific gravity, for example, will not result in also having all short tracheid trees, or all wide tracheids. Although there is some indication that thick walls and short tracheids tend to be carried along with high specific gravity, individual trees are found with nearly

Ranking of four selected trees by four characteristics indicating the lack of interdependence of the characteristics. The vertical position of each point indicates the relative value for that characteristic.

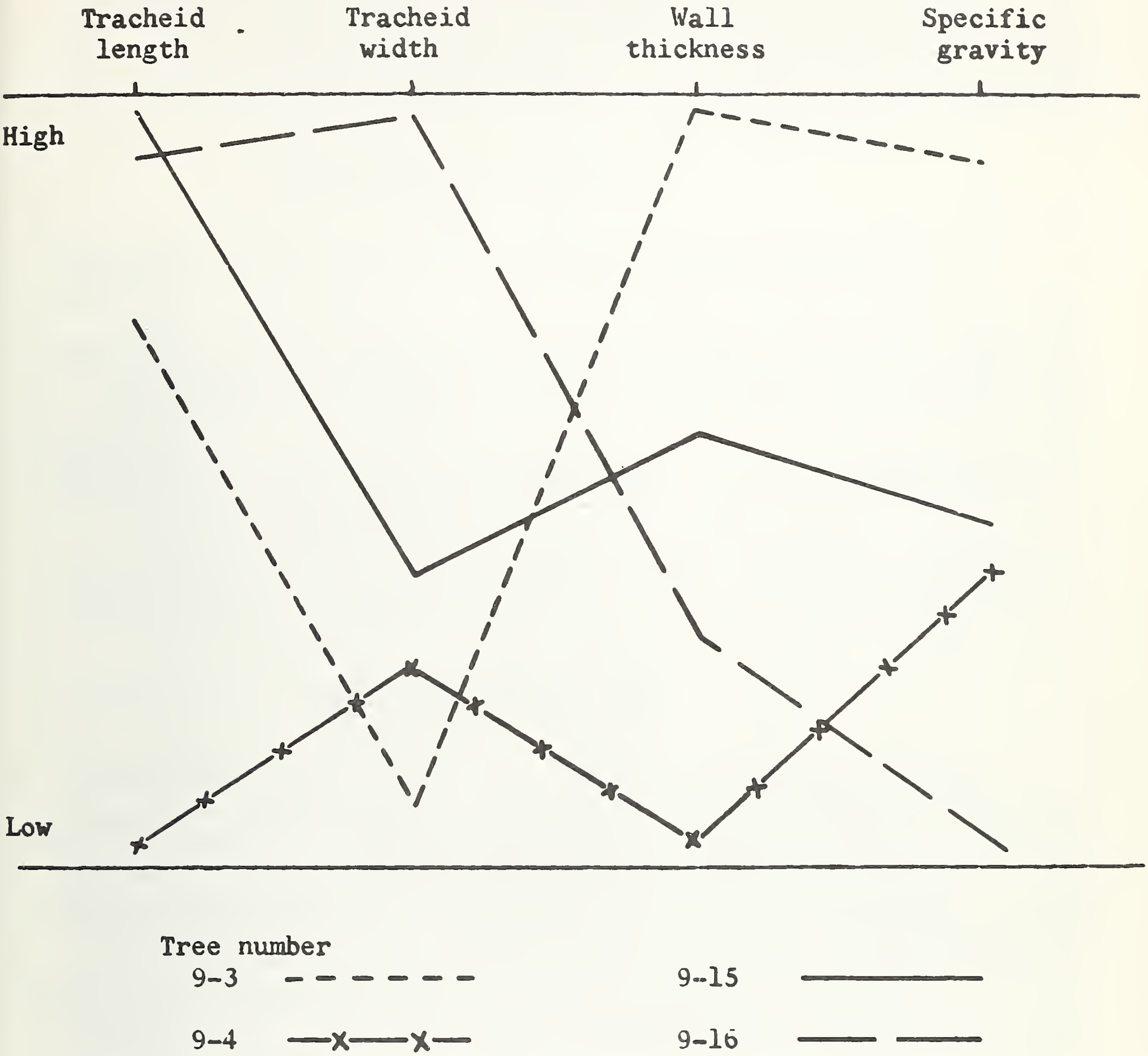

Figure 3. Graph showing lack of interdependence of four characters.

all possible combinations of factors. Since specific gravity itself is not a unit character, but the resultant of several characteristics, such as wall thickness and cell width, each of which appear to be fairly independent, indications would then be that gains in specific gravity would be modest. Heritabilities already in the literature (Zobel, 1961) indicate that very useful improvement can be made in specific gravity despite this complexity. With care, these gains can be achieved without sacrificing desired tracheid lengths or cell widths.

SOME MISCELLANEOUS WOOD PROPERTY RELATIONSHIPS

During the course of years, a mass of data has been obtained involving wood property relationships, both within trees and between trees. These data were not obtained as the result of studies specifically designed to determine such relationships, but were accumulated during analysis and assessment of the wood properties of the trees selected for use in the seed orchard program. This large amount of data gives a good opportunity to assess wood character variations within trees as well as relationships of certain characteristics among trees. The bulk of the data was obtained for loblolly pine trees selected for seed orchards of companies in the N. C. State--Industry Cooperative Tree Improvement Program. Trees were analyzed from a number of different sites and geographic regions within a 10-state area in the southeast. Although the trees analyzed are from numerous different environmental situations, they all have two things in common; i.e., all are the dominant, fastest growing, best formed trees in their respective areas, and all are somewhere near rotation age (30 to 50 years depending on the company involved).

Relationships of a Single Wood Characteristic Within a Tree

Specific gravity relationships of core wood to outer wood (i.e., wood near the tree center to that near the bark) have been reported several times. Correlations were from fairly high to quite high, and all reported figures are significant at the 1% level, showing that the specific gravity of the core wood is indicative of the specific gravity of the outer wood. In the present study, the correlation coefficient obtained was +.476 for trees from the Piedmont, +.506 for trees from the Coastal Plain, and +.517 for both physiographic provinces combined, representing measurements from a total of 313 trees. It is quite surprising that the core to outer wood specific gravity relationship turns out to be as strong and consistent as the data reported here indicated. The large amount of pitch and compression wood usually found near the center of the tree render accurate determination difficult.

In some preliminary studies, Kramer (1957), Zobel et al. (1960), and others have determined that there are within-tree relationships in tracheid length. Kramer found good correlation between tracheid lengths of wood formed in the 10th ring from the pith and that formed nearer the bark. From our studies, as well as from some made by Albemarle Paper Company, it would appear that the 15th ring is the earliest one that can be used for acceptable classification of a tree as to tracheid length. In our industrial work, we have made it a standard procedure to measure tracheid lengths (uncut tracheids) for the 15th and 30th ring from the pith, in order to determine an indicative tracheid length for the tree.

In a previous report (Zobel et al. 1960) the lengths of tracheids from the 15th and 30th rings were reported to be very highly correlated. Upon analyzing the data for 340 of our select trees, we have found correlation coefficients as shown in Table 5.

Table 5. Relationship of core to outer wood specific gravities and of 15-year and 30-year tracheids within the same tree. These measurements were made on the same group of trees.

Geographic Location	Specific Gravity		Tracheid Length	
	Number of Trees	"r" Value (core to outer)	Number of Trees	"r" Value (15 to 30)
Piedmont (Ala., Ga., S.C., N.C., and Va.)	114	.48**	134	.56**
Coastal Plain (same states)	199	.51**	206	.55**
All Trees Combined	313	.52**	340	.59**

The above indicates, then, that the length of the 15-year tracheids are a fairly good indication of the 30-year length, though certainly not precise enough for prediction purposes for any one individual tree. Use of tracheids from rings less than the 15th year would be desirable and probably will be feasible in later progeny tests. However, for an estimate of tracheid length characterizing the parent, we plan to continue to use 15 and 30-year tracheids. Near the center of the tree there is so much compression wood (about 50% of total volume of first 7 rings) and the tracheid length increase is so rapid from one year to the next, that working too near the pith can introduce chances for errors of very great magnitude.

Relationship Among Specific Gravity, Tracheid Length, and Growth Rate

It is our objective in this section to report interrelationships (by simple correlations) among the three variables of specific gravity, tracheid length, and growth rate. Data for these variables were obtained from the same group of trees for which within-tree variations were shown in the previous section (Table 5). As shown in Table 6, the data were calculated for Piedmont and Coastal Plain trees separately, and for the trees from both provinces combined.

Table 6. Interrelationships of the three variables of specific gravity, tracheid length, and growth rate for trees used in industrial seed orchards.

Relationship	Geographic Location	# of Trees	Correlation Coefficient
Specific gravity x tracheid length	Piedmont	149	-.152 NS
	Coastal Plain	213	-.070 NS
	All trees	362	-.160*
Specific gravity x rings per inch	Piedmont	153	.199**
	Coastal Plain	216	.026 NS
	All Trees	369	.117*
Tracheid length x rings per inch	Piedmont	130	-.017 NS
	Coastal Plain	206	.181**
	All trees	336	.105 NS

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* Significant at 5% level

** Significant at 1% level

NS Not statistically significant

Caution must be exercised in interpreting these data. As was pointed out previously, the correlation coefficient must be viewed from two angles: (1) is it statistically significant, and (2) is it large enough, numerically, to be of practical importance? The number of samples on which correlations are based is important; for example, the correlation coefficient of tracheid length to tracheid width (Table 3) for the 14 trees in the first section of this paper was .49 but not significant. However, specific gravity to tracheid length had r= -.160 (Table 6) which proved to be significant at the 5% level, because 361 trees were involved. The analysis that follows will take into consideration both interpretations of the correlation coefficient.

There is a consistent, though very small negative relationship between specific gravity and tracheid length. Although this relationship would suggest that higher specific gravity trees have shorter tracheids, the correlation coefficients are so small as to be of no practical importance (Table 6).

As has been found for other studies, when outer wood is compared, the relationship between specific gravity and growth rate is very low. In the present case, for all trees, the relationship was significant at the 5% level, but the correlation coefficient was so low that less than 2% of the variation in specific gravity is accounted for by growth rate; the coefficient indicates that slower growing trees have slightly higher specific gravities.

The difference in significance of correlation coefficients between Coastal Plain and Piedmont is of interest (Table 6); if it developed to be real, it would be of interest to attempt to explain. It is commonly assumed that in much of the Piedmont, soil moisture during the warm part of the year may be limiting. It is also assumed that plentiful soil moisture during summer would keep the tree growing for a longer period into the fall and thus would result in the trees having a higher specific gravity. However, a tree that would continue to grow longer in the fall probably would have faster growth if measured by rings per inch as was done in this study.[1] Thus, the result would be higher specific gravity with less rings per inch (faster growth), just opposite to the relationship reported in Table 6. Because of changes that occur within the tree, one might expect the rings-per-inch: specific-gravity relationship to be greatest for stands where age variation is the greatest. In the present study, however, the greatest age variation was in the Coastal plain, but the best relationship of growth rate to specific gravity was obtained in the Piedmont.

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[1] Although rings per inch is not a good measure of growth per se, it is satisfactory when the trees compared are of similar ages and when the time of growth involved in the measured period does not comprise greatly different weather "cycles".

It has commonly been considered that the faster growing trees usually have shorter tracheids than the slower growing trees. The data in Table 6 show this only for trees growing in the Piedmont. Although the correlation coefficient here is significant at the 1% level, only about 3% of the variation in tracheid length is accounted for by growth rate. Additional concepts regarding this relationship are given in the Discussion section that follows.

Discussion and Summary

From the two groups of data analyzed in this paper, and from the data in papers cited, it appears that (l) Within a tree at the breast height position on the bole:

(a) Specific gravity of the wood of the first formed rings (from 7 to 10) is highly correlated to that formed nearer the bark. Although highly statistically significant, the correlation values themselves are not numerically high. Actually, when one considers the potential experimental errors, the magnitude of errors that can be caused by pitch and compression wood near the tree center, the natural variation within a tree around the circumference of its trunk, it seems surprising to find correlation coefficients of the order of .5 to .6. Results of the relationship of wood near the pith to that near the bark have been reported a number of times by a number of different authors for a very large number of trees, and all show some degree of relationship.

(b) Although most studies have emphasized specific gravity, several have looked into the relationship of uncut tracheids formed near the tree center compared to those formed nearer the bark. Some authors have reported that the tracheid length near the pith can be used as predictive value for those formed farther out. Others indicate this predictive function not to be reliable unless the comparison is made with tracheids taken some distance from the pith, for example, from the 10th ring. Although we have not set up tests to specifically show this, some of our preliminary results have indicated that the tracheid length for the 15th and 30th ring best characterizes a tree. Therefore, correlations between the tracheid length at year 15 and at year 30 have been made and are always found to be highly correlated with statistically significant "r" values from .5 to .7. However, in the first section of this paper, comparisons were made between tracheid lengths, including cut ones, between the core segments comprising the first 7 rings from the pith and that formed later, and the correlations were highly significant statistically with "r" = .54. Just as for specific gravity, it is believed that the prevalence of compression wood especially affects the tracheid lengths from the rings nearest the pith. However, results reported here are for a large number of trees, and they suggest that a strong relationship between tracheid lengths formed at different distances from the pith may be expected.

(c) There is a highly statistically significant correlation (r = .61) between the thickness of tracheid walls at the center of the tree and of those formed farther out. Conversely, there was no correlation between the width of tracheids formed near the center and width of those formed farther out. These results must be considered only as preliminary indications, since they were for only 14 trees and the methodology for studying cell dimensions has not been as yet perfected.

(2) Between trees at the breast height location:

(a) For all characteristics studied, between-tree variation was very large, a phenomenon now becoming widely recognized. Often the difference between trees can be in the order of 100%; for example, the tree with the shortest tracheids at 30 years was 2.6 mm, while the tree with longest tracheids was 6.1 mm. The magnitude of this tree-to-tree variation cannot be overemphasized, and must be recognized when any wood property studies are made. This magnitude of variation makes it appear that the possibilities of improvement may be large.

(3) Relationships between different characteristics in trees sampled at breast height:

(a) Specific gravity x tracheid length. There is a very weak negative relationship between specific gravity and tracheid length. This means that trees with higher specific gravities will have slightly shorter tracheids. In a previous study (Zobel et al., 1960) obtained an "r" of -.16 for over 300 trees. In the present study, "r" of -.16 was also obtained for 362 trees, while "r" of -.3 was obtained for the 14 selected trees (but here with cut tracheids included in the sample rather than whole tracheids only). In a similar study, van Buijtenen et al. (1961) obtained an "r" of +.22 for 23 trees. These results make it obvious that the effect of specific gravity on tracheid length is very small. The possibility, or danger, of changing tracheid length by intense selection for specific gravity does not appear to be great.

(b) Specific gravity x tracheid width. Data for this relationship were obtain only for 14 trees, but seems reasonably strong with "r" equal to -.58. Thus, judged from this limited sample of 14 trees, it would appear that trees with higher specific gravities have distinctly narrower tracheids. This is not an unexpected relationship since it is entirely feasible that higher specific gravity may not be only the resultant of thicker cell walls, but also the resultant of having narrower cells, even though the walls are of the same thickness.

(c) Specific gravity x wall thickness. Again we have data only for 14 trees, but as would be expected, the trees having thicker cell walls also had higher specific gravities (r = .56). The correlation coefficient was not so high as might have been predicted, but it is quite evident that part of the specific gravity variation is due to the cell width as well as the wall thickness. (This outcome in turn, is all confounded with the percentage summer wood). This relationship is illustrated in Figure 4.

(d) *Tracheid length x tracheid width*. For the 14 trees studied, a correlation coefficient of .44 was obtained for tracheid length to width. This "4" is not statistically significant, due to the small number of trees involved, but it would indicate a possibility that trees having longer tracheids also have wider tracheids. Such a relationship could logically be expected.

(e) *Tracheid length x wall thickness*. Results are nearly identical to those for length x width, with a correlation coefficient of .49. Thus, it appears for the 14 trees involved in this study that the trees with longer tracheids will also have thicker-walled tracheids.

(f) *Tracheid width x wall thickness*. The "r" value here was .32, which was nonsignificant. Any trend present would suggest that the wider tracheids have thicker walls, but this relationship is weak for the 14 trees used in the present study.

(g) *Cellulose characteristics*. Cellulose characteristics seem to be independent of tracheid characteristics with the exception of wall thickness. Because of the gross method employed in these cellulose determinations, a cellulose wall-thickness relationship should be viewed with caution, and may simply reflect ease of penetration of the chlorite; however, the "r" value of .56 is of a magnitude that points toward the necessity for a better and more precise study of this relationship.

(h) *Growth rate x specific gravity*. In the present study, for 370 trees, it was found that the slower growing trees had slightly higher specific gravities, but growth rate accounted for less than 2% of the specific gravity difference. These results are similar to those in a recent report by Zobel *et al*. (1960), in which it was indicated that for over 300 trees also less than 2% of the variation in specific gravity could be accounted for by growth rate. Growth rate x specific gravity relationships are also in turn confounded with compression wood. It would seem to be a fair summary from our data to say, then, that on the basis of analyses of over 670 trees, all of which were either dominants or strong co-dominants in their respective stands, growth rate plays a very minor part in influencing specific gravity values.

(i) *Growth rate x tracheid length*. In the present study no significant relationship was found between growth rate and tracheid length with r = .105. This study has limited validity, however, since it is relating growth rate of the tree from the 10th year on to the length of tracheids at the 30th year. The objective of the present study was to determine, in a

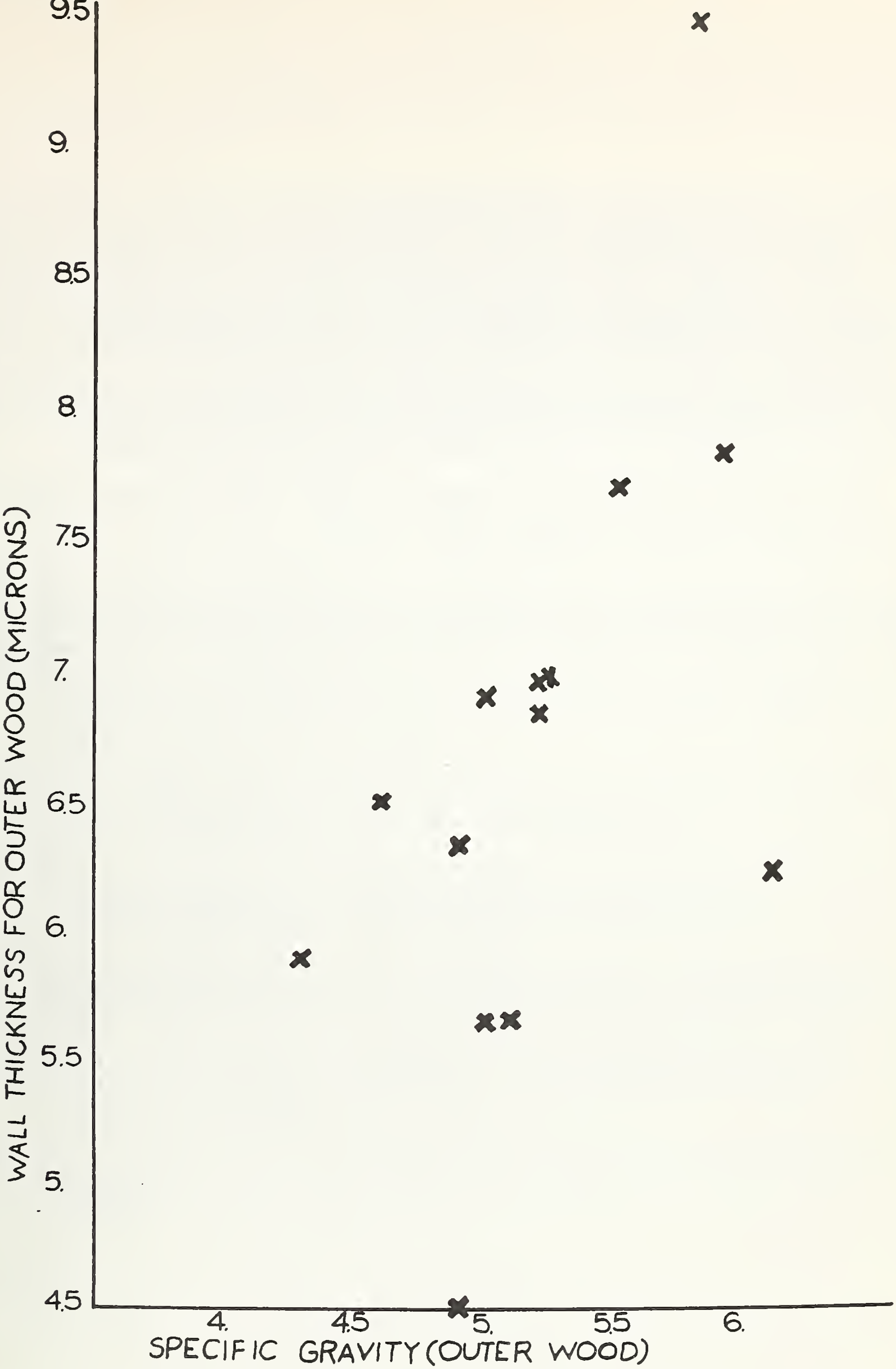

Figure 4. Graph showing relationship between wall thickness and specific gravity for 14 trees. r = .56.

broad way, if the fastest growing trees had different tracheid lengths than the slower growing ones, using length of tracheids at 30 years to characterize the tracheid length of the whole tree. Such a comparison would have general implications only. In a previous study, however, the controls were made on a more limited time period with growth of the 24th to 30th year compared to tracheid length at the 30th year. Under these conditions 10% of the variation of tracheid length could be accounted for by differences in growth rate. If individual years had been used, the relationship might have been even higher. From the data presented here, then, we can deduce that the fastest growing dominants and codominants do not have tracheids much different in length than the slower growing dominants and codominants.

It has been shown that a change in growth rate within a single tree (Bissett et al., 1951) is accompanied by a change in tracheid length.

(4) No multiple correlations were calculated, but it was found that trees with almost all possible tracheid characteristic combinations were found. This outcome indicates that there is considerable basis for hopes of developing strains of trees with varied wood characteristics.

LITERATURE CITED

1. Bissett, I. J. W., Dadswell, H. E., & Wardrop, A. B. 1951. Factors influencing tracheid length in conifer stems. Aust. For. 15: 17-30.

2. Dadswell, H. E., Fielding, J. M., Nicholls, J. W. P., & Brown, A. G. 1961. Tree-to-tree variations in gross heritability of wood characteristics of loblolly pine. TAPPI (In press)

3. Jackson, L. W. R. 1959. Loblolly pine tracheid length in relation to position in tree. Jour. For. 57: 366-367.

4. Kramer, P. R. 1957. Tracheid length variation in loblolly pine. Texas For. Ser. Tech. Report No. 10, 22p.

5. van Buijtenen, J. P., Zobel, B. J., & Joranson, P. N. 1961. Variation of some wood and pulp properties in an even-aged loblolly pine stand. TAPPI 44(2): 141-144.

6. Zobel, B. J. 1956. Genetic, growth, and environmental factors affecting specific gravity of loblolly pine. For. Prod. Jour. 6: 442-446.

7. Zob el, B. J. & Rhodes, R. R. 1955. Relationship of wood specific gravity in loblolly pine (Pinus taeda L.) to growth and environmental factors.

8. Zobel, B. J. & McElwee, R. L. 1958. Natural variation in wood specific gravity of loblolly pine and an analysis of contributing factors. TAPPI 42: 158-161.

9. Zobel, B. J., Thorbjornsen, E., & Henson, F. 1960. Geographic, site, and individual tree variation in wood properties of loblolly pine. Silvae Genetica 9(6): 149-158.

10. Zobel, B. J. 1961. Inheritance of wood properties in conifers. Silvae Genetica (In press).

POTENTIALS AND PROBLEMS OF HARDWOOD TREE IMPROVEMENT

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In preparing a paper on hardwood tree improvement for this Sixth Southern Forest Tree Improvement Conference, we wanted to contribute something other than the obvious truths. Everyone knows that there are great potentials for improving growth rate, quality, figure, resistance to insects and idseases and to inundation, and other desirable characteristics. The geneticists here understand many of the problems in applying their science to an oak tree or a poplar tree, just as they understand the problems of breeding pine trees. What more, then, can be said about the potentials and problems of hardwood tree improvement--particularly by a pair of unimproved tree-improvers?

In searching the literature and in conversing with others, we ran into such questions as, Where would a researcher start when he considers tree improvement with southern hardwoods? Where could he find records on flowering and seeding characteristics, or cytogenetic data? Where could he get information on methods of propagating the species, or on past breeding work? And perhaps most important of all, what facts could he use to assign work priority to selected species?

In an attempt to answer this multitude of questions, we have systematized as much data as we could find for the 20 southern hardwood species listed in table 1.

These 20 are perhaps the most valuable southern hardwoods at present, as judged by such factors as quality and growth, adaptability to particular sites, and utility. As in most literature reviews, some work may have been inadvertently omitted. If you know of published or unpublished data that we have missed, we sincerely hope you will tell us of it.

The information in table 1 is mainly from dendrology texts and various botanical publications (3, 7, 8, 9, 18, 23, 24, 25, 45, 61, 63, 66, 69, 71, 77), and from

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[1] The authors are members of the Stoneville (Mississippi) Research Center, maintained by the Southern Forest Experiment Station in cooperation with the Mississippi Agricultural Experiment Station and the Southern Hardwood Forest Research Group.

Table 1.--Flowering and seeding characteristics of 20 important southern hardwoods

Species	Type of flowers	Time of flowering	Time of seed maturity	Av. germinative capacity of stratified seed	Occurrence of good seed years 1/
				Percent	
Black cherry, Prunus serotina Ehrh.	Perfect	Mar.-June	June-Oct.	63	Annually
Black walnut, Juglans nigra L.	Monoecious	Apr.-June	Sept.-Oct.	75	Irregular
Black willow, Salix nigra Marsh.	Dioecious	Feb.-May	May-June	85	Annually
Cherrybark oak, Quercus falcata var. pagodaefolia Ell.	Monoecious	Feb.-Apr.	Sept.-Oct. 2/	38	Frequently
Eastern cottonwood, Populus deltoides Bartr.	Dioecious	Feb.-May	Apr.-June	88	Annually
Green ash, Fraxinus pennsylvanica Marsh.	"	Mar.-May	Sept.-Oct.	45	Frequently
Nuttall oak, Quercus nuttallii Palmer	Monoecious	Feb.-Apr.	Sept.-Oct. 2/	82	"
Overcup oak, Quercus lyrata Walt.	"	Mar.-Apr.	Sept.-Oct.	84	"
Shumard oak, Quercus shumardii Buckl.	"	Feb.-Apr.	Sept.-Oct. 2/	80	"
Silver maple, Acer saccharinum L.	Polygamo-dioecious	" "	Mar.-Apr.	76	"
Swamp chestnut oak, Quercus michauxii Nutt.	Monoecious	Mar.-May	Sept.-Oct.	87	Irregular
Sweet pecan, Carya illinoensis (Wangenh.) K. Koch	"	" "	" "	50	Frequently
Sweetgum, Liquidambar styraciflua L.	"	Feb.-May	Sept.-Nov.	80	Annually
Sycamore, Platanus occidentalis L.	"	Mar.-May	Sept.-Oct.	50	Frequently
Water oak, Quercus nigra L.	"	Feb.-Apr.	Sept.-Oct. 2/	61	"
Water tupelo, Nyssa aquatica L.	Polygamo-dioecious	Mar.-Apr.	Sept.-Oct.	50	Annually
White ash, Fraxinus americana L.	Dioecious	Apr.-May	Aug.-Oct.	38	Irregular
White oak, Quercus alba L.	Monoecious	Mar.-May	Sept.-Oct.	78	"
Willow oak, Quercus phellos L.	"	Feb.-May	Aug.-Oct. 2/	46	Frequently
Yellow-poplar, Liriodendron tulipifera L.	Perfect	Mar.-June	Sept.-Nov.	5	Irregular

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1/ Frequently--every 1 to 2 years; irregular--every 3 to 5 years with no set cycle.

2/ Maturing the year following pollination.

pamphlets on silvical characteristics (32, 33, 37, 40, 42, 51, 84, 85). Some material from files of the Stoneville Research Center is also included. It should be realized that the times given for flowering and seed maturity reflect latitudinal extremes. The occurrence of good seed years should also be taken with a grain of salt, as meteorological variations play a great part.

Notably absent from this table is a listing of minimum flowering ages, certainly a helpful tool to the plant breeded. The literature is largely silent on this subject, though it does report flowering of an 8-year-old black walnut (6), and a 7-year-old green ash (85). At Stoneville, W. M. Broadfoot has observed flowers on a 4-year-old cottonwood.

Several of the species are rather easy to propagate by vegetative means (tables 2, 3, and 4); some, notably sweetgum and the oaks, are difficult; and some, such as black cherry and water tupelo, just haven't been tried much. Horticulturists have worked a great deal with sweet pecan and black walnut, but almost always in the field of budding and grafting. At Stoneville we have recently initiated a long-range study in which we hope eventually to establish suitable methods for vegetative propagation of all southern hardwoods.

In table 5, on natural variation and tree improvement work, details of variation and hybridization are necessarily omitted, but literature references are noted. Many references on cottonwood and willow breeding are omitted, as this is a field in itself, and the material is easier to find than for other species. Considerable breeding work has been done with black walnut and sweet pecan by horticulturists, whose results will yield a wealth of information to the interested researcher on these two species. The same thing is true for black cherry, for while we have very little information on this species (10, 26) there is much horticultural literature on the genus *Prunus* (83).

It is in flower morphology, pollination, and cytogenetic characteristics that the gap in our knowledge is largest. Such basic information must be on hand before results of any tree improvement work can be completely interpreted. There are too many blank spaces and too many *probably*'s in table 6. Take, for instance, the natural variation of chromosome number. Jonathan Wright has found the northern geographic race of white ash to have a diploid chromosome number of 46, while the southern race may have a diploid number of 46, 92, or 138 (73). The entire genus of *Salix* is very variable in this respect (52). What other species or genera have similar variations? At the present time we do not know. But in view of the results that followed discovery of the famour triploid aspens (*Populus tremula* L.) in Sweden in the 1930's (52, 83), the possibility of similar conditions in any of our southern hardwoods is a tantalizing one for any tree improvement worker.

Table 2.--Ease of propagating hardwoods by cuttings[1]

Easy	Difficult	Unsuccessful	Unknown
Eastern cottonwood	Yellow-poplar	Water tupelo	Black cherry
Black willow	Nuttail oak	Water oak	Black walnut
Silver maple	Sweet pecan		Other oaks
Sycamore	Sweetgum		
Green ash[2]			
White ash[2]			

1. For further information, see: 16, 17, 35, 40, 43, 44, 62.
2. With cuttings from young tree seedlings. Difficult with cuttings from mature trees.

Table 3.--Ease of propagating hardwoods by air-layering[1]

Easy	Difficult	Unsuccessful	Unknown
Eastern cottonwood	Sweetgum	Yellow-poplar	Black walnut
Black willow	Sycamore	Cherrybark oak	Sweet pecan
Silver maple			Black cherry
Green ash			Water tupelo
White ash			Other oaks

1. For further information, see: 11, 21, 43, 62.

Table 4.--Ease of propagating hardwoods by budding and grafting[1]

Possible	Probably possible[2]	Unknown
Black walnut	Black willow	Sweetgum
Sweet pecan	All oaks	Sycamore
Eastern cottonwood		Black cherry
Green ash		Water tupelo
White ash		
Yellow-poplar		
Silver maple		

1. For further information, see: 19, 50, 62, 64, 68, 85.
2. Success with closely related species indicates the possibility.

Table 5.--Natural variation and tree improvement work in some important southern hardwoods

Species	Known species variation	Natural interspecific hybrids	Artificial hybridization	Other improvement work
Black cherry				Selection 1/, other (4, 36)
Black walnut	2-3 geog. races (28, 78, 80)		Some 2/ (34, 52, 54, 58, 88)	Seed source, selection 1/ (1, 12)
Black willow	Entire genus very variable (52)	1 known (30)	Some 3/ in the genus (52)	
Cherrybark oak		1 suspected		
Eastern cottonwood	2 geog. races, other variation (46, 76)		Very extensive (83)	Selection 1/
Green ash	3 geog. races, other variation (41, 72, 78, 83, 84, 86)	Suspected with white ash (83)	Some inter- and intraspecific (27, 59a, 76)	Seed source studies (41)
Nuttall oak				
Overcup oak		3 known, 1 suspected (30, 39)	NESS hybrids (19)	
Shumard oak	Some geog. variation (22, 82)	6 known (30)		
Silver maple	Extensive, even locally (74)		Some interspecific (2, 20, 59a, 75, 79)	
Swamp chestnut oak		1 known, 1 suspected (30, 39)		
Sweet pecan		4 known (7, 30)	Some 2/ intraspecific	
Sweetgum				Selection 1/
Sycamore		1 known (15, 23, 53, 67)		
Water oak	Some geog. variation (82)	5 known (30)		
Water tupelo				
White ash	3 geog. races, other variation (72, 73, 76, 78)	Suspected with green ash (83)	Some inter- and intraspecific (59a)	Selection 1/ (4)
White oak	Extensive, even locally (55, 83)	6 known (30, 59)	Some interspecific (57)	Selection 1/, other (13, 28)
Willow oak		8 known (7, 30)		
Yellow-poplar	Local variation, geog. races probable (28, 29, 31, 47, 60, 79)		Some intraspecific (79)	Seed source, selection 1/ (4, 5, 28, 31, 60)

1/ Implies selection of "plus trees" for any of several purposes.
2/ Nearly all for nut production.
3/ Mainly European work.

Table 6. --Some pollination and cytogenetic characteristics of southern hardwoods

Species	Normal diploid chromosome number	Natural variation of chromosomes	Natural pollinating agent	Irregularities encountered in breeding
Black cherry	32			
Black walnut	32 (52, 62)	In certain hybrids (52)		Parthenogenesis (87), dichogamy (52), metaxenia (54)
Black willow		Common in the genus (52)	Insects (23, 18)	
Cherrybark oak	Probably 24 (14)		Wind (7, 48)	
Eastern cottonwood	34 (62)		Wind (49)	Androgynous flowers reported (38)
Green ash	45 (62, 81)		Wind (85)	
Nuttall oak	Probably 24 (14)		Wind (7, 48)	
Overcup oak	Probably 24 (14)		Wind (7, 48)	
Shumard oak	Probably 24 (14)		Wind (7, 48)	
Silver maple	52 (62, 81)		Insects (75)	Sometimes self-pollinated (48), unusual flower structure (79)
Swamp chestnut oak	24 (52, 62)		Wind (7, 48)	
Sweet pecan	Probably 32 (62)		Wind (70)	Parthenogenesis indicated, some trees self-sterile (70)
Sweetgum	30 (62)			
Sycamore	42 (53, 62)			
Water oak	24 (52, 62)		Wind (7, 48)	
Water tupelo				
White ash	46--northern race (73)	46, 92, and 138 in southern race (73)	Wind (84)	
White oak	24 (52, 62)		Wind (7, 48)	Flowers only partly developed when pollinated (65), metaxenia (57)
Willow oak	Probably 24 (14)		Wind (7, 48)	
Yellow-poplar	38 (62)		Insects (79), mostly honey-bees (51)	Low self-compatibility (56), parthenocarpy exists (79)

In closing, we would like to point out a condition that we think needs alteration. A glance through the literature cited in this paper will show that more than 90 percent of the references are to work done in the northern United States or in Europe. Yet more than half of the Nation's hardwood timber is grown and cut in the South. There is no doubt about the potentials of growth and value in our southern hardwoods, but the problems for research and application are also present.

LITERATURE CITED

1. Anonymous.
   1961. New Walnut program. South. Lumberman 202(2518):42.

2. Al'Benski, A. V.
   1946. (Growth and winter-hardiness of interspecific hybrids of tree species) Nauchny Otchet VNIALMI za 1941-1942 g. Sel'khozgiz, Moscow, pp. 172-184. (In Russian) (Reviewed in Forestry Abs. 9:764. 1947).

3. Anderson, E., and Wheldon, C. M., Jr.
   1936. Studies in the genus Fraxinus. II. Data on the flowering and fruiting habits of three American species of ash--of possible economic importance in the production of rapid-growing trees. Jour. Hered. 27: 473-474.

4. Armstrong, M. M.
   1959. A note on the tree improvement activities of the Armstrong Forest Company. Sixth Northeast. Forest Tree Impr. Conf. Proc. 1958: 35.

5. Bailey, L. F.
   1948. Figured wood: a study of methods of production. Jour. Forestry 46:119-125, illus.

6. Brinkman, K. A.
   1957. Silvical characteristics of black walnut. U. S. Forest Serv. Cent. States Forest Expt. Sta. Misc. Release 22, 15 pp., illus.

7. Brown, C. A.
   1945. Louisiana trees and shrubs. La. Forestry Comn. Bul. 1, 262 pp., illus.

8. Carpenter, I. W., and Guard, A. T.
   1950. Some effects of cross-pollination on seed production and hybrid vigor of tuliptree. Jour. Forestry 48: 852-855, illus.

9. Chisman, H. H.
1955. The natural hybrid oaks of Pennsylvania. Pa. Agr. Expt. Sta. Res. Paper 22, 4 pp.

10. Darlington, C. D., and Wylie, A. P.
1955. Chromosome atlas of flowering plants. 519 pp. London.

11. Doran, W. L.
1957. Propagation of woody plants by cuttings. Mass. Agr. Expt. Sta. Bul. 491, 99 pp.

12. Dorman, K. W.
1952. Directory of forest genetic activities in the South. U. S. Forest Serv. Southeast. Forest Expt. Sta. Sta. Paper 17, 17 pp.

13. Downs, A. A.
1949. Low forking in white oak sprouts may be hereditary. Jour. Forestry 47: 736.

14. Duffield, J. W.
1940. Chromosome counts in Quercus. Amer. Jour. Bot. 27:787-788.

15. ________ and Snyder, E. B.
1958. Benefits from hybridizing American forest tree species. Jour. Forestry 56:809-815, illus.

16. Enright, L. J.
1958. Propagation of several species of Acer by cuttings. Jour. Forestry 56:426-428, illus.

17. ________
1959. Vegetative propagation of forest trees. Sixth Northeast. Forest Tree Impr. Conf. Proc. 1958: 3-7, illus.

18. Fernald, M. L.
1950. Gray's manual of botany. Ed. 8, 1,632 pp., illus. New York.

19. Flory, W. S., Jr., and Brison, F. R.
1942. Propagation of a rapid growing and semi-evergreen hybrid oak. Tex. Agr. Expt. Sta. Bul. 612, 32 pp., illus.

20. Freeman, O. M.
1941. A red maple, silver maple hybrid. Jour. Hered. 32:11-14.

21. Frohlich, H. J.
1957. Die autovegetative Vermehrung durch Luftablegerverfahren. Silvae Genetica 6:143-147, illus.

22. Gabriel, W. J.
1958. Genetic differences in juvenile Shumard oak. U. S. Forest Serv. Northeast. Forest Expt. Sta. Res. Note 81, 3pp.

23. Harlow, W. M., and Harrar, E. S.
1937. Textbook of dendrology. 527 pp., illus. New York.

24. Harrar, E. S., and Harrar, J. G.
1946. Guide to southern trees. 712 pp., illus. New York.

25. Isbell, C. L.
1928. Growth studies of the pecan. Ala. Agr. Expt. Sta. Bul. 226, 63 pp., illus.

26. Klaehn, F. U., and Neu, R. L.
1960. Hardwood pollen study. Silvae Genetica 9: 33-64, illus.

27. Lazarescu, C.
1956. (Contribution to the method of obtaining and breeding ashtree hybrids.) Rev. Biol. (Bucarest) 1:117-126. (In Rumanian) (Reviewed in Forestry Abs. 18(1):123. 1957)

28. Limstrom, G. A.
1955. Current forest tree improvement research in the Central States. Lake States Forest Tree Impr. Conf. Proc. 1955: 37-41. Lake States Forest Expt. Sta. Misc. Rpt. 40, 108 pp.

29. ________
1959. Yellow-poplar seed quality varies by seed trees, stands, and years. U. S. Forestry Serv. Cent. States Forest Expt. Sta. Sta. Note 134, 2 pp.

30. Little, E. L., Jr.
1953. Check list of native and naturalized trees of the United States (including Alaska). U. S. Dept. Agr. Agr. Handb. 41, 472 pp.

31. Lotti, T.
1955. Yellow-poplar height growth affected by seed source. U. S. Dept. Agr. Tree Planters' Notes 22:3, illus.

32. ________
1957. Silvical characteristics of cherrybark oak. U. S. Forest Serv. Southeast. Forest Expt. Sta. Sta. Paper 88, 9 pp., illus.

33. ________
1960. Silvical characteristics of swamp chestnut oak. U. S. Forest Serv. Southeast. Forest Expt. Sta. Sta. Paper 110, 8 pp., illus.

34. McKay, J. W.
1959. Techniques in breeding new varieties of orchard trees. Sixth Northeast. Forest Tree Impr. Conf. Proc. 1958: 21-25.

35. Maisenhelder, L. C.
1957. Propagation of some Delta hardwoods by rooting. Fourth South. Forest Tree Impr. Conf. Proc. 1957: 55-58.

36. Marquis, R. W.
1955. Report for the Northeastern Forest Experiment Station to the Second Lake States Forest Tree Improvement Conference. Lake States Forest Tree Impr. Conf. Proc. 1955: 23-28. Lake States Forest Expt. Sta. Misc. Rpt. 40, 108 pp.

37. Martindale, D. L.
1958. Silvical characteristics of sweetgum. U. S. Forest Serv. Southeast. Forest Expt. Sta. Sta. Paper 90, 14 pp., ilus.

38. May, S.
1959. (A case of bisexuality in *Populus deltoides*.) Cellulosa e Carta 10(7): 6-8. (In Italian) (Reviewed in Forestry Abs. 21(1):259. 1960.)

39. Melvin, L.
1956. A new hybrid oak from the Piedmont of North Carolina. Jour. Elisha Mitchell Sci. Soc. 72(2):346-347.

40. Merz, R. W.
1958. Silvical characteristics of American sycamore. U. S. Forest Serv. Cent. States Forest Expt. Sta. Misc. Release 26, 20 pp., illus.

41. Meuli, L. J., and Shirley, H. L.
1937. The effect of seed origin on drought resistance of green ash in the Prairie-Plains states. Jour. Forestry 35:1060-1062, illus.

42. Minckler, L.S.
1957. Silvical characteristics of white oak. U. S. Forest Serv. Cent. States Forest Expt. Sta. Misc. Release 21, 18 pp., illus.

43. Nelson, T. C.
1957. Rooting and air-layering some southern hardwoods. Fourth South. Forest Tree Impr. Conf. Proc. 1957: 51-54.

44. ________ and Martindale, D. L.
1957. Rooting American sycamore cuttings. Jour. Forestry 55:532.

45. Pauley, S. S.
1948. Sex and vigor in *Populus*. Sci. 108:302-303.

46. ________
1958. Photoperiodism in relation to tree improvement. The physiology of Forest Trees, ed. Thimann. Pp. 557-571, illus. New York.

47. Perry, G. S., and Coover, C. A.
1933. Seed source and quality. Jour. Forestry 31: 19-25.

48. Piatnitsky, S. S.
1934. (Experiments on self-pollination of Larix, Acer, and Quercus.) Trudy Botan. Inst. Akad. Nauk. S.S.S.R. 4(1):297-318. (In Russian.) (U.S. Forest Serv. Div. Silvics Transl. 290, 22 pp.).

49. Piccarolo, G.
1952. (The poplar tree. Practical roles of cultivation). Agr. Pubs., Rome. (In Italian) (Transl. reprinted in U. S. Dept. Com. 1954. Study of newsprint expansion: Part II. Newsprint production from hardwoods. Second Prog. Rpt. to U. S. House of Represent. Judiciary Com., pp. 293-332)

50. Pitcher, J. A.
1960. Heteroplastic grafting in the genera *Acer*, *Fraxinus*, *Picea*, and *Abies*. Seventh Northeast. Forest Tree Impr. Conf. Proc. 1959: 52-57.

51. Renshaw, J. F., and Doolittle, W. T.
1958. Silvical characteristics of yellow-poplar. U. S. Forest Serv. Southeast. Forest Expt. Sta. Sta. Paper 89, 18 pp., illus.

52. Richens, R. H.
1945. Forest tree breeding and genetics. Imp. Agr. Bur. Joint Pub. 8, 79 pp.

53. Sax, K.
1933. Species hybrids in Platanus and Campsis. Jour. Arnold Arboretum 14: 274-278.

54. Scepotjev, F. L.
1950. (Metaxenia in Juglans nigra.) Priroda, Moskva 39(11):59-61. (In Russian) (Reviewed in Forestry Abs. 13(1):86. 1951).

55. Scheffer, T. C., Englerth, G. H., and Duncan, C. G.
1949. Decay resistance of seven native oaks. Jour. Agr. Res. 78: 129-152, illus.

56. Schreiner, E. J.
1953. Possibilities of inbreeding, selective intraspecific breeding, racial and species hybridization, and polyploidy. First Northeast. Forest Tree Impr. Conf. Proc. 1953: 64-68, illus.

57. ________ and Duffield, J. W.
1942. Metaxenia in an oak species cross. Jour. Hered. 33:97-98, illus.

58. Schuster, C. E.
1937. Differences in heterosis of walnut hybrids. Jour. Hered. 28:216-217.

59. Silliman, F. E., and Leisner, R. S.
1958. An analysis of a colony of hybrid oaks. Amer. Jour. Bot. 45:730-736.

59a) Sixth Northeastern Forest Tree Improvement Conference.
1959. Proceedings. 45 pp.

60. Sluder, E. R.
1960. Early results from a geographic seed source study of yellow-poplar. U. S. Forest Serv. Southeast. Forest Expt. Sta. Res. Note 150, 2pp., illus.

61. Small, J. K.
1933. Manual of the southeastern flora. 1,554 pp., illus. Chapel Hill, N.C.

62. Spector, W. S. (Editor)
1956. Handbook of biological data. 584 pp. Philadelphia, Pa.

63. Stuckey, H. P.
1916. The two groups of varieties of the Hicora pecan and their relation to self-sterility. Ga. Agr. Expt. Sta. Bul. 124, 21 pp., illus.

64. Swedish Association for Breeding of Forest Trees.
1942. Annual report, 1942. Svensk Papp Tidn. 45:300-307, 324-327, 382-383, 404-409, 519-522, 542-543. (In Swedish) (Reviewed in Forestry Abs. 5(2):92. 1943).

65. Turkel, H. S., Rebuck, A. L., and Grove, A. R., Jr.
1955. Floral morphology of white oak. Penn. Agr. Expt. Sta. Bul. 593, 14 pp., illus.

66. U. S. Forest Service.
1948. Woody-plant seed manual. U. S. Dept. Agr. Misc. Pub. 654, 416 pp., illus.

67. Walther, E.
1935. Genetic constitution of host plant as a factor in pest control. Monthly Bul. Calif. Dept. Agr. 24:242-244.

68. Wiesehuegel, E. G., Zarger, T. G., and Hatmaker, J. F.
1957. Handling valuable nursery stock. Fourth South. Forest Tree Impr. Conf. Proc. 1957: 81-90.

69. Woodroof, J. G.
1924. The development of pecan buds and the quantitative production of pollen. Ga. Agr. Expt. Sta. Bul. 144:133-161, illus.

70. ________ and Woodroof, N. C.
1930. Abnormalities in pecans. I. Abnormalities in pecan flowers. Jour. Hered. 21:39-44, illus.

71. ________ Woodroof, N. C., and Bailey, J. E.
1928. Unfruitfulness of the pecan. Ga. Agr. Expt. Sta. Bul. 148, 40 pp., illus.

72. Wright, J. W.
1944. Ecotypic differentiation in red ash. Jour. Forestry 42:591-597.

73. ________
1944. Genotypic variation in white ash. Jour. Forestry 42:489-495.

74. ________
1949. Local genetic variation in silver maple. Jour. Forestry 47: 300-302.

75. ________
1953. Breeding of hardwoods. Second South. Forest Tree Impr. Conf. Rpt. 153: 1-13. Univ. Fla. Tech. Rpt. 9.

76. ________
1953. Interspecific hybridization in spruce, maple, and ash at the Northeastern Forest Experiment Station. First Northeast. Forest Tree Impr. Conf. Proc. 1953: 77-81.

77. ________
1953. Notes on flowering and fruiting of northeastern trees. Northeast. Forest Expt. Sta. Sta. Paper 60, 38 pp., illus.

78. ________
1953. Racial variation and individual tree selection in the Northeast. First Northeast. Forest Tree Impr. Conf. Proc. 1953: 20-25.

79. ________
1953. Summary of tree-breeding experiments by the Northeastern Forest Experiment Station 1947-1950. Northeast. Forest Expt. Sta. Sta. Paper 56, 47 pp.

80. ________
1954. Preliminary report on a study of races in black walnut. Jour. Forestry 52:673-675.

81. ________
1957. New chromosome counts in *Acer* and *Fraxinus*. Morris Arboretum Bul. 8:33-34.

82. ———
1957. Studies to improve shade trees. Amer. Nurseryman 106(9): 56, 57, 60-63, illus.

83. ———
1958. Possibilities of genetic improvement of the southern bottomland hardwoods. Seventh Ann. La. State Univ. Forestry Symposium Proc. 1958: 27-34.

84. Wright, J. W.
1959. Silvical characteristics of green ash. U. S. Forest Serv. Northeast. Forest Expt. Sta. Sta. Paper 126, 18 pp., illus.

85. ———
1959. Silvical characteristics of white ash. U. S. Forest Serv. Northeast. Forest Expt. Sta. Sta. Paper 123, 19 pp., illus.

86. ——— Bingham, R. T., and Dorman, K. W.
1958. Genetic variation within geographic ecotypes of forest trees and its role in tree improvement. Jour. Forestry 56: 803-808.

87. Zarubin, A. F.
1949. (On the possibility of parthenogenesis in *Juglans regia* and *J. nigra*.) Priroda, Moskva 38(10): 64-65. (In Russian). (Reviewed in Forestry Abs. 12(1): 105. 1950)

88. Zuravskaja, E. I.
1958. (A *Juglans* hybrid in Dublyany village (near Lvov).) Lesn. Hoz. 11(9): 75-76. (In Russian) (Reviewed in Forestry Abs. 21(2): 1482. 1960).

SUMMARY OF THE SIXTH SOUTHERN FOREST TREE IMPROVEMENT CONFERENCE

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It is a real pleasure to be back in Florida, and to see so many of my friends who are connected with tree improvement activities throughout the South. After helping to start off the Southern Forest Tree Improvement Committee just ten years ago, it has been most gratifying to hear Dr. Kaufman's excellent account of "A Decade of Progress in Tree Improvement," and all these other accounts of current progress. And believe me there is no better way to catch up than to consent to prepare a summary of the entire meeting. This summary will have served its purpose if it helps to etch upon your mind, as it has on mine, some of the new knowledge that all these speakers have assembled for us.

Wakeley's report on "Results of the Southwide Pine Seed Source Study through 1960 - 61" is the first comprehensive report on this vast study. The report substantiates earlier evidence of very limited racial variation in slash pine. The other three species did show distinct racial variation. In loblolly and shortleaf pine, this variation was considerably greater among origins from a north-south transect than from an east-west transect. If loblolly or shortleaf is moved too far toward either the north or south portions of its range, height growth is reduced.

Local stocks were above average in performance, but were usually excelled in survival by certain individual westerly sources, and in height growth by certain individual westerly sources, and in height growth by certain individual easterly or southerly sources.

Fusiform rust resistance of loblolly pine was greater in stocks of westerly origin than those of easterly origin, regardless of where planted.

This study is a real accomplishment of the Southern Forest Tree Improvement Committee, and a real tribute to the efforts of Phil Wakeley and all his many cooperators in the undertaking.

Eyvind Thor, in "Variation Patterns in Natural Stands of Loblolly Pine," reported differences in the seeds, cones, and leaves of loblolly pine from the Eastern Shore of Virginia to eastern Texas. In all of 18 characteristics studied, he found that a considerable proportion of the total variation was accounted for by tree-to-tree variation within seed source areas. Of the 13 traits which showed highly significant differences between areas, the majority did not show any regional trend. Five traits did show some degree of pattern in their regional variation.

The strongest clinal pattern was an increase in seed-coat thickness from Texas toward the east and from the interior toward the southeastern coast, in agreement with the trend in precipitation-evaporation ratio. A similar clinal pattern was found in stomatal frequency, increasing toward the east. This is consistent with the stomatal pattern Mergen found in slash pine.

Seed form, cone weight, and cotyledon number all showed unique geographic patterns with no obvious biological significance.

Thomas Zarger's "Ten-Year Results on a Cooperative Loblolly Pine Seed Source Test" covers roughly the span of the life of this committee. The study is one of several in which a few seed sources seemed to do best at most of the planting locations, and generally outperformed the local strain. In general, the TVA study the inland sources survived better than the Atlantic Coastal Plain sources and are recommended for planting beyond the natural range in the interior. Inland sources were also superior in diameter growth, but their initial superiority in height growth at 5 years of age had evaporated 5 years later.

Various people have sought to find or develop a type of longleaf pine seedling with a fibrous root system in an attempt to improve the low survival of longleaf after planting on poor sites. In his talk on "Racial Variation of Root Form of Longleaf Pine Seedlings," E. B. Snyder told us that seedlings from origins west of south-central Georgia had fewer roots and lower total root length than those from farther east. This difference might reflect the selective action of lower summer and autumn rainfall to the west.

In "Physiological Aspects of Racial Variation," Thomas O. Perry said that the results of past research reveal racial variation in the following physiological responses: photoperiod requirement, duration of growing season, drought resistance, upland versus lowland and maritime versus inland habitats, altitude, winter chilling requirements, nutrient requirements, and soil requirements. He gave several instances of racial variation in southern pines and red maple in response to photoperiod, light intensity, and day and night temperature. For example, northern sources of red maple had lower optima of both day and night temperature than southern sources. In loblolly pine, Maryland sources grew poorly in Florida unless given extended daylength to simulate that of their home in Maryland.

Doctor Perry concludes that genetic strains can be developed that will give superior (but perhaps not optimal) performance over a fairly large geographic province. Experience from agronomic crops indicates that two or three improved genetic strains will adequately serve the needs of a fairly large state.

In his philosophical paper "Selection as a Method of Tree Improvement" Keith Dorman makes a good case for a more careful selection of priorities to guarantee rapid progress toward genetic improvement. He stresses the gains that can be made through simple roguing of stands, through seed-production areas, through better knowledge of individual and racial variation, through concentrating more effort on the most important species and the most significant traits, and through performing selection under the most favorable conditions of stand and site uniformity. He asks practicing foresters to keep the pressure on geneticists to give them useful techniques as well as estimates of costs and benefits of tree improvement. Researchers must realize that their job is to make complicated things simple, not to make simple things complicated.

In their paper on "Statistical Aspects of Progeny Testing," Evans, Barber, and Squillace reap a considerable harvest of lessons from progeny tests established in the past decade. Their first plea is that anyone making a progeny test establish in his mind a minimum level of difference which he will consider meaningful. Only then can an appropriate test be designed and interpreted. In fact the authors ask the Tree Improvement Committee to prepare guides to the least meaningful differences in respect to traits that are important in progeny testing.

Their second main point is that it is futile to install progeny tests in randomized block designs if the blocks are too big. Their evidence is that blocks 1 acre in size are entirely too big for areas of patchy soil variation such as the Georgia Piedmont. This means that the number of trees per plot or the number of progenies or both must somehow be kept down.

The authors deny the appropriateness of the single-tree plot for ordinary use in progeny test, first, because it leads into the statistical complications of missing-value techniques; second, because it fails to show how the progenies develop in a group of their own kind; and third, because recognized statistical tests which presume normal distribution of error may fail to apply to data from single-tree plots.

They recommend a 25-tree plot because the coefficient of variation for many individual traits such as height tends to level off at about 20 surviving trees per plot. Where there are more different progenies than can be gotten into the allowable block size with 25-tree plots the authors suggest a 2-stage process of a screening test with all progeny, followed by a more rigid test of the most promising ones. Incomplete block designs are another alternative, though a risky one.

The authors plead for the release of file data which will contribute to our knowledge of the variability encountered in previous progeny tests. Their final plea is that all second-stage progeny tests be repeated in both time and space to take account of the influence of year-to-year and place-to-place variations that affect growth and survival.

Concerning "Inheritance of Vigor in Slash Pine," Peters and Goddard reported that both open- and control-pollinated progenies of slash pine parents selected for high vigor exceeded average progenies in this trait. Heritability of vigor in their study was very roughly estimated at 15 percent. They confirmed other reports of reduced vigor from self-pollination. Among the controlled pollinated progenies there were definite indications of variation in specific combining ability.

Squillace and Bengtson, in "Inheritance of Gum Yield and Other Characteristics of Slash Pine," give some specific inheritance information from the plantations of rooted cuttings and control-pollinated and wind-pollinated progeny tests at Lake City. They conclude that heritability is very strong for gum yield (45 to 90 percent) moderately strong for bark thickness, diameter, and volume growth (5 to 67 percent), weak for total height at 10 to 15 years (5 to 16 percent) and weak to moderately strong for crown width (12 to 48 percent). The average heritability of perhaps 55 percent for gum yield indicates very good promise for genetic improvement in this trait.

"Growth, Crown Form, and Fusiform Rust Resistance in Open-Pollinated Slash Pine Progenies" were reported by David VanHaverbeke for John C. Barber. This work was initiated by Keith Dorman at the Ida Cason Callaway Foundation in the early 1950's. Barber's paper assesses both the biological results and the validity of progeny testing methods. As for methods of progeny testing, he found consistently that the block X progeny-group interaction was significant. This means that the progeny groups are more sensitive to site variations than had been expected, and that sensitive tests will require using several relatively uniform test sites. He also found, when he attempted to correct growth rate for stand density, that the progenies that survived best grew fastest in diameter and height, even though the number of competing trees on each plot was greater. It was impossible to tell what portion of this relationship is attributable to inherent vigor and what portion to site variation. If it is vigor, then mortality and vigor are confounded, and any adjustment of progeny test growth data for differences between progenies in stand density will be very difficult.

A significant though not unexpected finding is that branch length and branch diameter are negatively correlated with branch angle. Thus we can select trees with which have more nearly horizontal branches and expect that these branches will tend to be shorter in length and smaller in diameter.

In these studies the greatest degree of crook was found in progeny from crooked parents. Progenies from open-pollinated seed collected in different years gave similar estimates of the parent trees in such traits as rust resistance. There was a weak tendency for the faster-growing progeny groups to be less resistant to fusiform rust, but the correlation is low enough to be negligible in its bearing on selection work. Even under severe field conditions, some of the faster growing progenies remain free of rust infection. Rust cankers inhibit growth, so cankered trees must not be used in estimating the inherent vigor of progenies. The author feels he was successful in estimating greneral crown characteristics from measurements of single whorls on progenies 7 or 8 years old. The most variable characteristics studied were height and diameter, which is no doubt a reflection of their greater sensitivity to variation in site.

F. F. Jewell's paper covered "Results of Artificially Testing Intra- and Interspecies Southern Pine Hybrids for Rust Resistance." Some crosses of pairs of rust-free slash pine parents produced progeny with increased resistance, and other crosses did not. Hybrids of the resistant species shortleaf pine with susceptible species have shown no galled individuals in limited field trials. However, under intensive artificial inoculation, the different progeny groups from four slash X shortleaf crosses resulted in a full range from 4 to 92 percent of galled individuals. Apparently rust resistance in interspecies shortleaf hybrids is more complicated than the simple dominance for resistance in shortleaf assumed earlier. In order to produce relatively resistant progeny it is probably necessary to use parent trees that have shown the ability to transmit resistance in earlier trials.

Carl Maisenhelder's "Selection of Populus Clones for Southern Bottom Lands" describes the program of selection in cottonwood at the Stoneville (Mississippi) southern hardwood research project of the Southern Forest Experiment Station. In view of the tremendous growth potential of cottonwood in our southern bottom lands, and the ease with which it can be propagated vegetatively, I view this as one of the very best opportunities for tree improvement in the United States, and perhaps the best of all for the development of highly intensive culture in combination with genetic improvement. Early results indicate that of Euramerican hybrids, I 214 (a spontaneous cross between cottonwood and European black poplar) grows best at Stoneville. But selections of native cottonwood with such fine rustic names as Catfish No. 8 have outstripped the most famous hybrids from Europe, and one native cottonwood is 30 feet tall and 4.8 inches d.b.h. at 2 years of age from the cutting. Future research will be concentrated on the development of elite types with superior growth, quality, pest resistance, and site adaptability.

"Advances in Tools and Techniques of Tree Improvement" were discussed and illustrated by Franklin C. Cech. He described present tree-climbing devices, with particular emphasis on the evolution of truck- and trailer-mounted ladders. He also described the latest equipment for pollination and for removal of wood samples from living trees, including a reversible 1-inch electric drill for extracting large increment cores.

Campbell and Wakeley presented specific suggestions concerning "Possible Refinements in Controlled Pollination of Southern Pines." First, put on bags before buds enlarge to avoid contamination. Second, bagged flowers can be pollinated at any stage from 2 (buds large) to 5 (Flowers at maximum receptivity) inclusive, though yields from pollination at stages 4 (Flowers partly open) and 5 are the most certain and abundant. Third, it is far more difficult than has been realized to tell when flowers have in fact ceased to be receptive. If contamination is intolerable, flowers must not be debagged until far into or past the conventional stage 6 (flowers closed). The authors also found that pollen germinating as low as 65 percent in laboratory tests may be well worth using in attempts to make certain greatly desired crosses. High laboratory germination is not essential for success in crossing.

Francois Mergen's paper on"Natural and Induced Flowering in Young Pine Trees" makes several new contributions to our knowledge of early flowering. Among these are the observations that Mugo pine seedlings have flowered when less than 1 year old, that there are precocious ecotypes in jack pine, that interspecific hybrids may flower earlier than the parent species, and that flowering could be induced in 2-year-old white pine hybrids and Scotch pine by various manipulations of temperature, humidity, and nutrition. The manner in which these factors go about producing their effect on cell differentiation is still a challenging mystery for future research.

Merkel and Ebel's report "Cone and Seed Insects and their Control" identifies the main culprits on southern pines in Florida as coneworms, seedworms, and a species of pine thrips which attacks the succulent flowers of slash pine. Tentative spray schedules for the control of these insects are given. Another possibility for control of the pine seedworm, particularly in isolated seed orchards, is to collect the entire cone crop, infested and sound. This reduces the population to zero, but the researchers do not yet know how soon the moths (*Laspeyresia anaranjada*) would reinvade the seed orchard.

The paper on "Interrelationship of Wood Properties in Loblolly Pine" by Zobel, McElwee, and Browne substantiates the general correlation in wood properties between the younger and older wood laid down by the same tree, except for width of tracheids. The magnitude and genetic importance of anatomical differences *between trees* was emphasized. These tree-to-tree differences in such properties as tracheid length can amount to as much as 100 percent.

The most significant part of this paper examines the interrelationships among the various wood properties in loblolly pine. The strongest relationships were between specific gravity and cell wall thickness (positive). Among the cell dimensions, tracheid width, length, and wall thickness were only weakly related to each other. Cellulose characteristics were only weakly related to cell dimensions. Faster growth rate tended to be associated with lower specific gravity and shorter tracheids, but this relationship was very weak and was overshadowed by the large differences among trees.

No correlations of more than two wood characteristics were calculated, but the authors found that almost all possible combinations of characteristics occurred in different trees. From this they conclude that we can expect to be able to produce strains of trees with almost any specified wood quality without having to accept undesired characteristics as a bonus.

McKnight and Bonner in "Potentials and Problems of Hardwood Tree Improvement" summarize the important information available on flowering, seeding characteristics, and cytogenetic data for twenty selected species of southern hardwoods, such as cottonwood, willow, sweetgum, oaks, and yellow-poplar, and others.

All in all, this sample of recent progress indicates that we have gone a long way in forest genetics research and tree improvement programs since that time 10 years ago when plans were made for an expected attendance of 25 or 30 people at the First Southern Forest Tree Improvement Conference. Now there are 48 professional workers in this field in the South. Perhaps the most impressive thing about the accomplishments of the past decade has been the cooperation of all forestry agencies, particularly through the Southern Forest Tree Improvement Committee. The massive South-wide seed-source study is a fine example of this cooperation.

Where do we go from here? I feel that the southern pine and hardwood forest region should have a tree improvement program second to none in the world. This area is the largest body of really good-quality timber-producing land north of the Tropic of Cancer, where most of the world's markets lie. It has a half-billion dollar pulpwood crop annually, plants narly 2 billion trees a year, and has some sites which, with the best plant materials and most intensive culture, should produce up to 500 cubic feet per acre per year. Its level topography and broad areas of uniform climate mean that a reasonably small number of improved strains will serve the region. This is far from true in the mountains that dot most of our timber-growing areas.

You folks are largely the ones who will determine how fast the genetic improvement of timber trees will move ahead in this ideal setting. It is your efforts that will determine how much progress we will be able to record when we meet for our twentieth anniversary in 1971.

Publications and Reports Prepared in Cooperation With the Committee on Southern Forest Tree Improvement:

Report of the first southern conference on forest tree improvement. Atlanta, Georgia, January 9-10, 1951. U. S. Forest Serv., Atlanta, Ga. (Mimeo)*

Proposal for a cooperative study of geographic sources of southern pine seed. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. Southern Forest Expt. Sta. 1951. (Mimeo.)*

Standardized working plan for local tests of seed source. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. Southern Forest Expt. Sta. 1951. (Mimeo)

Hereditary variation as the basis for selecting superior forest trees. Subcommittee on Tree Selection and Breeding. Keith W. Dorman, Chairman, Southeastern Forest Expt. Sta. Paper 15. 1952.

Directory of forest genetic activities in the South. Subcommittee on Tree Selection and Breeding, Keith W. Dorman, Chairman. Southeastern Forest Expt. Sta. Paper 17. 1952.

Suggested projects in genetic improvement of southern forest trees. Committee on Southern Forest Tree Improvement. Southeastern Forest Expt. Sta. Paper 20. 1952.

Testing tree progeny. A guide prepared by the Subcommittee on Progeny Testing, E. G. Wiesehuegel, Chairman. Tennessee Valley Authority, Technical Note No. 14. 1952.

Report of the second southern conference on forest tree improvement. U. S. Forest Serv., Atlanta, Ga. 1953. (Mimeo)*

Progress in study of pine races. Philip C. Wakeley. Southern Lumberman 187(2345): 137-140. December 15, 1953.

The role of genetics in southern forest management. Special subcommittee of the Committee on Southern Forest Tree Improvement. Bruce Zobel, Chairman. Pt. 1, Forest Farmer 14(1): 4-6, 14-15. Pt. 2, Forest Farmer 14(2):8, 14-19. Pt. 3, Forest Farmer 14(3):8-9, 14-15. (Reprint, 11 pp. 1954).

Proceedings of third southern conference on forest tree improvement. Southern Forest Expt. Sta. 1955.

Better seed for better southern forests. Subcommittee on Genetic Control of Seed, T. E. Maki, Chairman. N. C. State College School of Forestry Tech. Rpt. 9. 1955.

Forest tree improvement for the South. Committee on Southern Forest Tree Improvement, T. E. Bercaw, Chairman. 1955.

Supplement No. 1 to the original working plan of September 12, 1952, for the southwide pine seed source study. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman.

Time of flowering and seed ripening in southern pines. Subcommittee on Tree Selection and Breeding, Keith W. Dorman, Chairman, and John C. Barber, Southeastern Forest Expt. Sta. Paper 72. 1956.

Proceedings of the fourth southern conference on forest tree improvement, University of Georgia. 1957.

Pest occurances in 35 of the southwide pine seed source study plantations during the first three years. Southern Forest Expt. Sta. 1957.

Proceedings of the fifth southern conference on forest tree improvement. North Carolina State College, Raleigh. 1959.

Minimum standards for progeny-testing southern forest trees for seed certification purposes. Subcommittee on Progeny Testing for Seed Certification Purposes. Philip C. Wakeley, Chairman. Southern Forest Expt. Sta., 20 pp. 1960.

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* These reports are out of print.